A TAXONOMIC AND ECOLOGIC STUDY OF THE RIVERBOTTOM FOREST ON ST. MARY RIVER, LEE CREEK, AND BELLY RIVER IN SOUTHWESTERN ALBERTA, CANADA

Robert K. Shaw[1]

Abstract.— The riverbottom forest community of St. Mary River, Lee Creek, and Belly River in southwestern Alberta, Canada, is a unique ecological entity characterized by poplar species having their major Alberta distribution along these streams. Stands in the community are dominated by three tree species, six shrub species, and nine herb species. Establishment of the community is dependent on climate and substrate; destruction is the result of progressive lateral stream-flow erosion. Soils are sandy loams above gravel, with pH values of 7.7 to 8.0 and soluble salt concentrations of 176 to 458 parts per million. Trees in mature stands averaged 23.0 cm in diameter and 40 years in age; maximum tree age was 250 years. The vascular flora consists of 291 species of which 41 are woody and 250 herbaceous. One species (*Prunus nigra* Ait.) new to Alberta and range extensions for 12 species are cited. There are no true community endemic species. Recreational and livestock-raising uses are present community modifiers. Fire is not important in current forest dynamics.

The riverbottom forest community of southwestern Alberta, Canada, is usually less than 0.8 km in width and occurs on only certain lengths of each stream. It has been utilized for pasture and, to a minor extent, for firewood and timber, leaving much of the woodland free from excessive disturbance. This study treats several aspects of the riverbottom forest community including the vascular flora, community stratification and composition, successional patterns, seasonal aspect, climate, geography, geology, and soils.

St. Mary River, Lee Creek, and Belly River originate in alpine tundra (elevation 2,000-3,200 m) on the Lewis Range of the Rocky Mountains in Glacier National Park, Montana (Fig. 1). From alpine tundra these streams flow northeast into the Province of Alberta, Canada, through montane forest and aspen parkland into the treeless stretches of fescue prairie (elevation 900-1,400 m) where, along the stream courses, the poplar-dominated riverbottom forest community becomes a unique ecological entity (Fig. 2).

St. Mary River drains about 3,440 km², Lee Creek about 290 km², and Belly River about 1,235 km² of northwestern Montana and southwestern Alberta.

Monthly water flow in all three streams varies widely throughout the year. From late July through autumn and winter the flow is fairly constant, but during March warmer weather causes snow melt in the foothills and on the lower mountain slopes to increase stream flow. The most rapid melting of deep mountain snow occurs in late May and early June. This coincides with the season of highest precipitation when stream flow is swollen to its maximum, which is four to five times the winter flow rate. Stream flow generally peaks rapidly in late May or early June followed by a rapid decline throughout July. Maximum flow in any year seldom persists for more than 24 hours. Irrigation water is in low demand at the high run-off season, and the six small weirs and diversions on the three streams exert little control on downstream flooding. In spite of these uses, near normal flow does prevail in the three streams in all months of the year except July, August, and September.

Pollution of the waters varies. No in-

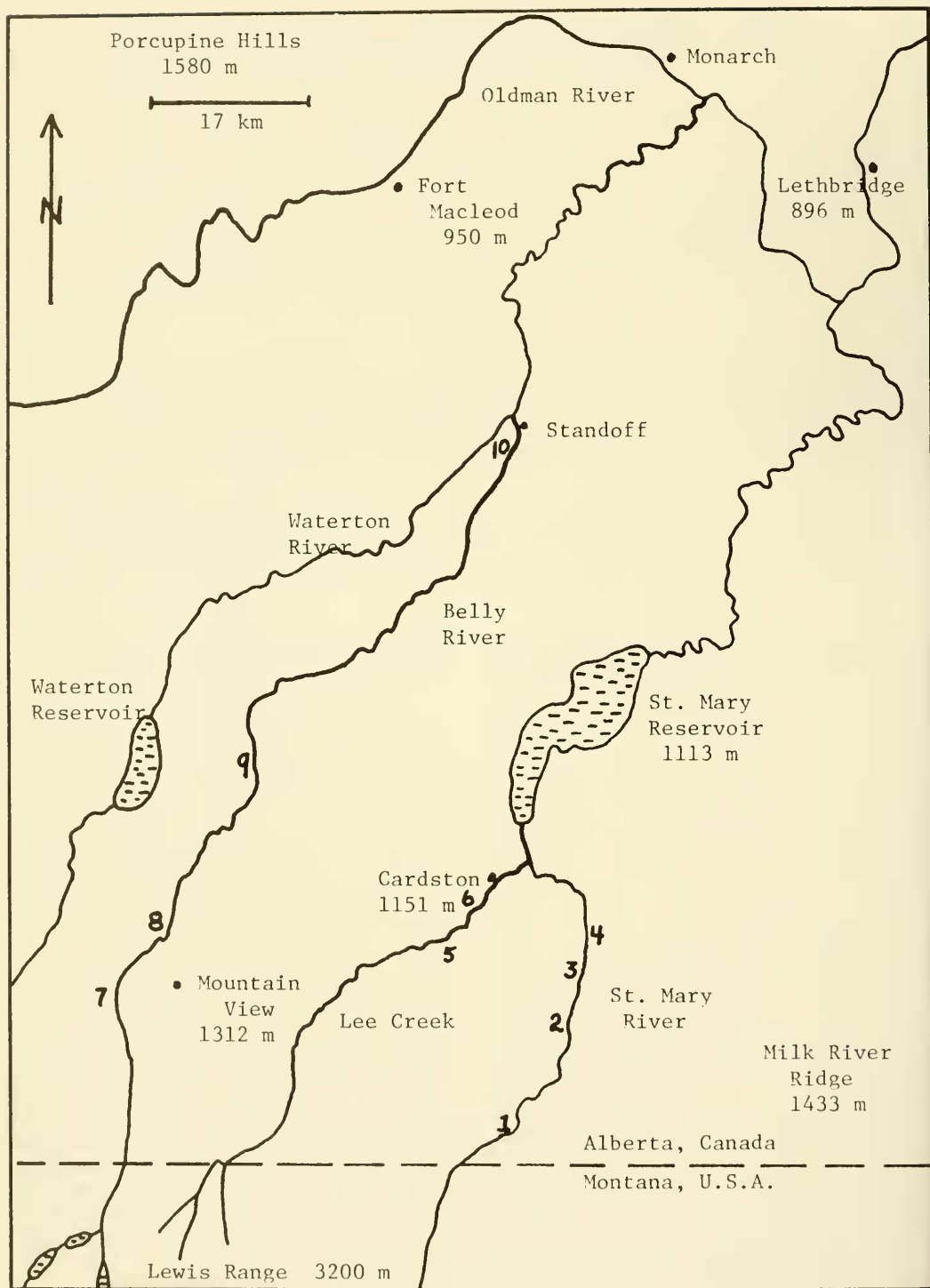[1]Box 364, Cardston, Alberta, Canada.

Fig. 1. Streams of southwestern Alberta, Canada. The major ecologic and taxonomic study sites are numbered 1 through 10.
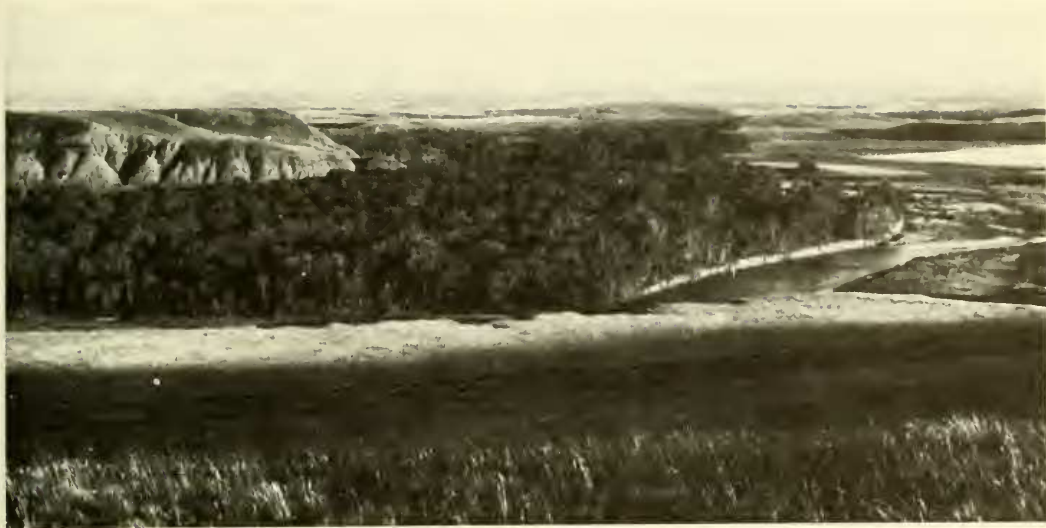
Fig. 2. Site 4 on St. Mary River, a typical climax stand of riverbottom forest on the second terrace. The background farmland is on the third terrace, and the foreground road crosses the fourth terrace grassland.

dustrial wastes reach these streams, al-though municipal sewage and some agri-cultural feedlot effluent cause local prob-lems. Early snowmelt combined with per-colation and leaching of water through old vegetation and manure on the up-lands causes discoloration and objec-tionable odor in the water during March and April of each year. High runoff from rain and melting snow in late May and early June produces a high particulate content in the water at this time. For the rest of the year stream water in St. Mary River, Lee Creek, and Belly River tends to be clear, clean, and free from con-taminants.

GEOLOGY AND GEOGRAPHY

The headwaters of the three streams originate on the Continental Divide over geological formations of the Belt Series in the Lewis Range of the Rocky Moun-tains (Wyatt 1939). These strata, nearly all of sedimentary origin, were formed during the Proterozoic Era of 510,000,000 years ago when much of western Alberta, eastern British Columbia, Montana, and Idaho were covered by a shallow sea. These rocks, with a maximum thickness of more than 6,100 m, are in the form of a large syncline, the east edge of which forms the Lewis Range. The greatest thick-nesses of limestone show numerous fossils of calcareous algae and primitive marine plants.

The mountains themselves, of more re-cent origin, are about 58,000,000 years old. They resulted when tremendous crustal forces, principally from the west, were directed against the geosyncline. The Proterozoic rocks were uplifted and moved some 80 km to the east where they were warped into a great anticline, the Lewis Overthrust, which overlies the younger Cretaceous shales and sandstones of the plains. It is because of the Lewis Over-

thrust that there are no significant foot-hills on the east side of the Lewis Range.

During Miocene and Pliocene time the mountains were deeply eroded by streams. Several thousand meters of Belt rocks were removed during the course of valley formation. Near the close of Pliocene time the climate cooled, vegetation disappeared, and mountain glaciers formed from the snow and began to move down the stream-carved valleys where they met the con-tinental glaciers advancing from the north.

The prairie section of St. Mary River, Lee Creek, and Belly River flows through and over a variety of consolidated and unconsolidated deposits, from the trans-ported Belt series rocks of Proterozoic time to the more recent Cretaceous series. The geological formations which occur at the surface or immediately below the un-consolidated deposits in the plains and foothills zone of southwest Alberta are Cretaceous and Tertiary in age. A large area of southwestern Alberta prairie, which includes the Porcupine Hills and Willow Creek formations, is underlain by formations of Tertiary age. Through Cardston and southward to the interna-tional boundary, the soft sandy shales and sands have influenced the soils where they occur near the present surface.

The St. Mary River nonmarine strata underlie the Willow Creek formation of early Tertiary age and represent the uppermost Cretaceous strata in southwest Alberta. This formation consists mainly of highly calcareous light gray sandstones and sandy shales. Irregular bedding and crossbedding are common. Soils influenced by these beds have a pronounced lime con-tent. Freshwater oyster shells and coal beds are common in this formation. Much of the prairie section of the three study streams cuts through the St. Mary River formation.

The marine Bearpaw formation consists mainly of dark gray clay shales and sandy shales. A large area of Bearpaw extends from Township 1 Range 21 north-ward to Township 8 Ranges 22 and 23. Much of the lower half of St. Mary River, where there is no riverbottom forest, flows through this formation. A narrow band of Bearpaw shale extends from Cardston south beyond Kimball, and from Kimball upstream on St. Mary River to the mouth of Coalmine Coulee.

Much of southwestern Alberta is ve-neered with glacial deposits (Wyatt 1939). Glaciation was general over most of the area. There is also widespread dis-tribution of reworked glacial deposits as well as alluvial and lacustrine deposits transported by rivers and creeks. Retreat of the glaciers is presumed to have oc-curred for the last time about 9,000 years ago (Dyson 1949).

Soils on the prairie section of south-western Alberta are generally fertile. As-pen parkland and some adjacent fescue prairie are in the black soil zone and east of this are the shallow black soils which grade gradually into dark brown soils of the mixed grass prairie and short-grass plains. The dark brown and most of the shallow black zones underlie tree-less prairie. The soils along the river and creek bottoms are of alluvial deposition and some, still liable to frequent flood-ing, are quite variable in texture and utilization (Wyatt 1939).

Undoubtedly the Lewis Range of the Rocky Mountains on the west side of the area is the most prominent topographic feature of the landscape. In this part of Alberta the break from mountains to plains is fairly rapid, there being no wide range of foothills. The Porcupine Hills (elevation 1,580 m) is a prominent topo-graphic feature bordering Oldman River on the north. East of St. Mary River the land gradually rises to Milk River Ridge, which has the appearance of a high north-south plateau with a maximum ele-vation of 1,433 m. Between these three landmarks lies the area of study, which is in the nature of a large plain of level to rolling land ranging in elevation from 900 to 1,200 m.

Climate

Bounded on the west by the mountains and foothills of the Rocky Mountains, the whole of the three prairie provinces—Al-berta, Saskatchewan, and Manitoba—con-sists of vast plains deeply cut by river valleys and gently sloping toward the east and northeast. The western mountains form a fairly effective barrier to the mar-itime influence of the Pacific, and at the same time the area is left exposed to the inflow of cold Arctic air masses from the north (Canada 1969).

Summers are normally warm, but winters are usually long and intensely cold. Throughout southwestern Alberta mean temperatures are below 0 C from November through March. Winter cold across the province increases from southwest to northeast. Winter temperatures on the prairies may vary widely from month to month during a single winter, or from year to year, depending on the character and path of air masses passing over the region. In some winters, with a steady flow of cold polar air, a cold spell may last for several weeks. On the other hand, in other winters the southerly flow of Arctic air may be quite weak allowing air of Pacific origin to move eastward at the surface, thus bringing mild weather.

Winter temperatures in the lee of the Rockies reflect the warming effect of the "chinook" wind which occurs from the Northwest Territories to the United States but is most pronounced in southern Alberta with effects noticeable as far east as Regina, Saskatchewan. Characteristically, the chinook occurs as a westerly or southwesterly wind and is brought about by the subsidence east of the western mountain ranges of maritime Polar air from the Pacific. This air is cooled adiabatically at the saturated lapse-rate in its ascent over the mountains. In its descent to the plains, however, it is warmed again adiabatically at the dry lapse-rate which is twice the cooling rate during the ascent. Consequently, this air reaches the foothills at a much higher temperature than it had at a corresponding level on the western slopes. The chinook is most striking when it occurs following a cold wave that has been accompanied by snow. The sky clears abruptly and temperatures may rise as much as 30 C in 24 hours. The bright sunshine and above-freezing temperatures cause the snow to melt rapidly and some plants may be stimulated to begin growth prematurely with subsequent deleterious effects.

Temperatures rise rapidly from winter to summer and decline with equal rapidity from summer to winter. The transition periods are usually confined to April and October. Monthly mean temperatures in southwestern Alberta are above 10 C for the five months May to September. Extreme maximum temperatures have exceeded 38 C over most of the prairies.

Temperatures may fall to 0 C or lower in every month of the year in less favored locations in the southern prairies.

The average frost-free period in southern Alberta ranges from 80 to 120 days, which is critically close to the minimum required for cultivated grain crops to reach maturity. The growing season to which the native flora has adapted is 85 days at Mountain View, 100 days at Cardston, 110 days at Lethbridge, and 120 days at Medicine Hat, the progressive lengthening occurring with increasing distance from the mountains and with decreasing altitude (Longley 1968).

The prairie provinces are fortunate in receiving a high average of sunshine for the latitude; the annual total ranges from 2,000 to 2,350 hours in the prairies. July is the sunniest month with total exceeding 300 hours at most stations in southern Alberta. December is the dullest month of the year with all stations showing total less than 100 hours. There is a noticeable tendency for the sky to be either cloudless or completely overcast on the prairie (Canada 1969).

Lying in the center of the continent and shielded from the Pacific by the western mountain ranges, the Canadian prairies lack available sources for abundant precipitation. The region is favored, however, by the fact that cyclonic activity is fairly vigorous and the hot summers are conducive to convection. The heaviest precipitation results from the lifting of extensive masses of moist air moving northward from the Gulf of Mexico and adjoining regions. Droughts are usually associated with abnormally low pressure in the Northwest Territories, which produces only a weak southward flow of cold air.

In marked contrast to the Pacific Coast with its winter maximum, the prairies have a rainy season from late May to early October, although no season is without some precipitation. The light precipitation is somewhat mitigated by the fact that 60 to 75 percent of the year's precipitation (45.8 cm at Cardston) falls during the growing season when it can be utilized by plants.

Precipitation shows wide variations from year to year, with differences between the extreme annual amounts exceeding the mean annual total in most

areas. Monthly precipitation totals are more often in deficit than in excess. June and July are most likely to have high rainfall totals.

Winter snowfall is comparatively light with amounts ranging from 76 to 127 cm over the central prairies. This amount increases to 180 cm in the foothills of the Rockies and at least twice that amount in the highest ranges. Snow may fall in any month except July and August, although measurable snow is unusual in June. The first snow cover usually appears in late October and snow disappears in early April. A combination of heavy snowfall and wind causes drift buildup in coulees and along the streams throughout winter.

Literature Review

The riverbottom forest community in southwestern Alberta is found on stream floodplains which show characteristics of Melton's classification. Melton (1936) proposed one category containing floodplains seldom or never subject to overbank floods. These lack sedimentary deposits on the surface, and lateral corrosion results in the formation of meander loops. A second category included floodplains frequently subject to over-bank floods with considerable sedimentary deposits on the surface.

In a study of the Coeur d'Alene River floodplain in Idaho, Humphrey (1924) came to the conclusion that the vegetation on the floodplain of that river had spread from the south and east into Idaho because of the constancy of the moisture factor along the river floodplain. Actual transfer of disseminules probably came about through winds and the movements of birds.

Lee (1945) reported 40 species of tall trees, 9 species of small trees, and 14 species of shrubs from the floodplain forest of the White River in Indiana. A well developed small tree-shrub layer was lacking in the stratigraphic development of the forest and stands along the river showed striking similarity even though the river passed through four botanical areas of striking difference in the upland forest. Microclimate was thought to be of more importance than macroclimate.

Ware and Penfound (1949) studied the floodplain of the South Canadian River in Oklahoma and found sparse vegetation due to annual destruction by floods, shifting of sand, a high rate of evaporation, the intense heat of the sand surface, and the drying out of sand. A total of 85 species of plants was found. Dominant tree species were *Populus deltoides*, *Salix interior*, and *Tamarix gallica*.

The Mississippi River floodplain in northwestern Tennessee has been given special study by Shelford (1954). The two dominant large tree species were *Populus deltoides* and *Salix nigra*. The climate of the area was favorable for the rapid growth of trees on the higher terraces of the floodplain. Annual rainfall was 112 to 125 cm and the mean annual temperature was 16 C. Nearly every year two or more early stages of the floodplain forest were inundated, the length of submergence varying from one week to two and one-half months. Usually flooding came early in the spring but sometimes as late as May or June. The herb layer was usually poorly developed. Cottonwoods of 50 to 60 cm diameter at breast height showed 20 annual growth rings in the Donaldson area north of Tiptonville. In the Reelfoot Lake area cottonwoods grew in diameter at the rate of 2.1 cm or more per year, but in Iowa, farther north, growth was measured at only 1.0 cm per year. The cottonwood stand near the Tiptonville Ferry was estimated about 40 years old, counting from the time the cottonwoods were seedlings. The area was a sandbar island in the river 52 years earlier. Estimated time for the complete development of the climax Tulip-Oak Forest was 600 years.

In a survey of the vegetation of Alberta, Moss (1955) described the flats of rivers in the prairie parkland of southwestern Alberta as being commonly dominated by poplars and willows with associated birch, alder, and a variable assemblage of herbaceous species. The leading poplar species designated were *Populus angustifolia*, *P. acuminata*, *P. sargentii*, *P. trichocarpa* (near the mountains), and *P. balsamifera*. There was evidence of hybridization between certain of the cottonwoods and also between the two balsam poplars. The chief willow species indicated were *Salix lutea*, *S. caudata*, *S.*

interior var. *pedicellata*, *S. melanopsis*, and *S. amygdaloides*.

Wistendahl (1958) described the floodplain of the Raritan River, New Jersey, as flowing through three of four geologic provinces with floods unpredictable from 0 to 16 days per year, March having the most floods. High precipitation occurred in the summer when floods were scarce. Succession trends on new alluvium reflected the dynamics of stream action. The dominant tree species on the levee were willow, river birch, sycamore, and box elder.

Hosner (1958) found that cottonwood (*Populus deltoides*) seedlings could survive only with fewer than eight days complete inundation by flood water with variable rates of recovery.

Weaver (1960) reported that the pioneer tree species on the floodplain of the Central Missouri Valley were *Salix amygdaloides*, *S. nigra*, and *Populus sargentii*. The floodplains were subject to occasional or frequent flooding but were moderately to well drained between overflows. He concluded that it was not the soil type alone that determined the kind and amount of native vegetation but rather aeration and constancy of water supply of these mostly productive soils that directly affected their vegetation.

Lindsay et al. (1961) reported 629 species of plants from a study of the vegetation and environment along the Wabash and Tippecanoe Rivers in Indiana. Pioneer tree species were cottonwoods (*Populus* spp.) and black willow (*Salix nigra*). A medium-sized island largely built by a major flood supported both cottonwoods and willows up to 33 cm diameter after 15 years. There were from four to seven stages in succession from pioneer grass-forb to the floodplain edaphic climax.

Early taxonomic studies, which included accounts of the plant species of stream valleys, include the work of Macoun (1883-1909) on plants of the western prairies, Standley (1921) on flora of Glacier National Park in Montana, and Rydberg (1922, 1932) on the floras of the Rocky Mountains and plains and prairies of central North America. An early edition of Native Trees of Canada (1956) gave good accounts of tree species taxonomy and distribution. In 1955 Moss presented an overview of

the vegetation of Alberta which preceded his monumental work (1959), the Flora of Alberta, a most comprehensive work for the time and still the most useful taxonomic tool for the province. Supplementary accounts of southwest Alberta plants are to be found in Budd (1957), Booth (1950), and Booth and Wright (1959).

Some help in understanding the plants of the upper reaches of Belly River and Lee Creek was provided by Breitung's (1957) enumeration of the plants of Waterton Lakes National Park, Alberta.

Popular treatments including some of the riverbottom species are Cormack's (1967) Wild Flowers of Alberta and Kuijt's (1972) Common Coulee Plants of Southern Alberta. A detailed and complete account of the northern great plains flora was provided in Boivin's (1967) Flora of the Prairie Provinces.

Specific treatment of the woody vascular plants found along southwest Alberta streams was done in Shaw's (1968) Guide to the Woody Plants of the Lee Creek Valley and (1972) Guide to the Woody Plants of the Prairies, Foothills and Valleys of Southwest Alberta.

Brayshaw (1965) has provided the necessary treatment of native poplars of southern Alberta and their hybrids, which is most valuable in both taxonomic and ecologic evaluations of streamside communities.

METHODS AND MATERIALS

The riverbottom forest community of St. Mary River, Lee Creek, and Belly River was chosen for this ecologic and taxonomic study of the vascular flora because of a personal interest of long standing in these streams and their vegetation. Discounting plant collecting and ecosystem observations spanning the decade 1959 to 1969, the actual planned research for this paper covered the years 1970 through 1973. Intensive field data collection was carried out during the growing seasons of 1970, 1971, and 1972 with followup and fill-in studies completed by autumn 1973.

Study sites along the stream systems were chosen with two purposes in mind: (1) intensive plant collection only, and (2) both plant collection and ecosystem data collection. Within this frame

of reference, sites were evaluated from headwaters to outlet on each of the three study streams during the summer of 1970. Some sites were discarded because they did not fall within the riverbottom forest community proper, being in upstream transition zones. Others were not selected because of community alteration by livestock overgrazing, timber cutting, farmstead site, and cattle feedyards. Final sites meeting standards of reasonable expectation of similarity to pre-1870 climax community aspect numbered 19. A major objective of the study was to describe the species of vascular plants and their ecological relationships in the apparent edaphic-climatic climax of the present.

There were 10 numbered major ecologic-taxonomic sites (Fig. 1). Four were chosen on St. Mary River. From upstream to downstream, with the assigned name and legal description, the sites were (1) Cook's Ranch, SW¼ S9 T1 R25 W4; (2) east of Aetna, SE¼ S19 T2 R24 W4; (3) Cardwell's Island, NE¼ S30 T2 R24 W4; and (4) Woolford Park, NE¼ S31 T2 R24 W4.

On Lee Creek there were two major study sites and these in upstream to downstream order were (5) Town Dam, NE¼ S26 T2 R26 W4 (Fig. 3); and (6) Slaughter Hole, NW¼ S4 T3 R25 W4.

Belly River had four major study sites and from upstream to downstream they were (7) Highway 5 bridge, SW¼ S17 T2 R28 W4; (8) Hillspring Park, NE¼ and NW¼ S13 T3 R28 W4; (9) Glenwood Bridge, SW¼ S6 T5 R26 W4; and (10) Standoff, S27 S28 S33 S34 T6 R25 W4 and S2 T7 R25 W4.

Nine minor taxonomic sites were chosen. On St. Mary River these were at Coalmine Coulee, SE¼ S22 T1 R25 W4; Kimball Park, SW¼ S1 T2 R25 W4; east of Cardston, unsurveyed Blood Indian Reserve; Christensen Farm, SW¼ S27 T5 R23 W4; and Blood Reserve Cut-off, SW¼ S30 T6 R22 W4.

Minor sites on Lee Creek were the Dugway, S5 T1 R27 W4; the Narrows, S20 T2 R26 W4; and Cardston, town of Cardston.

The one minor site on Belly River was at the Belly River-Oldman River confluence, S27 S28 T9 R23 W4.

Since prior to this study no precise

Fig. 3. Site 5 on Lee Creek with the climax stand of riverbottom forest on the second terrace at right and a pioneer site on the first terrace gravel bar at left.

evaluation of the vascular flora of the riverbottom forest had ever been made, intensive plant collecting was done throughout the growing season, beginning in early May and ending in late September. Important sites were collected thoroughly from five to seven times to insure complete records of all species. Specimens were preserved according to standard herbarium practice. After careful checking and comparison with known material, all specimens collected—some 1500 numbers—were deposited in the Herbarium of Brigham Young University, Provo, Utah (BRY). A duplicate set of specimens remains in my private herbarium at Cardston, Alberta.

Taxonomy of the poplars follows Brayshaw (1965), the genus *Cryptantha* after Higgins (1971), the genera *Astragalus* and *Oxytropis* follow Welsh (1960), and the remainder are after Moss (1959), Boivin (1967), Booth (1950), and Booth and Wright (1959).

After several field trials, using various methods, a standard procedure for obtaining numerical data on forest stands evolved. Information leading to density, dominance, and frequency was desired throughout. Each forest stand was sampled by following a predetermined pattern—travel parallel to the stream, sample at intervals, interrupt the interval whenever nonforest terrain was crossed. Field data were recorded on data sheets similar to those suggested by Cox (1967).

Data on trees, tree reproduction, and clumped shrubs were best obtained by using the point-centered quarter method recommended by Cottam and Curtis (1956). Point-to-plant distance determination by tape measure proved quite difficult because of the brush; so an optical range finder (Edscorp), also recommended by Cottam and Curtis (1956), was substituted for the tape with the operator standing beside the plant and sighting back to a two-meter rod painted alternately red and green at decimeter intervals set at the point of quadrant intersection. The travel interval between points was 30 m, and three strata—trees, tree reproduction, and clumped shrubs —were sampled from the same point.

Dominance calculations were based on diameter-breast-high for trees, tree reproduction dominance on height, and canopy diameter for clumped shrubs. All measurements were based on estimates with frequent tape measure checks to insure reliability.

The line-intercept method, using a 30-meter steel tape placed at right angles to the line of travel at 30 m intervals, proved to be satisfactory for obtaining information on clonal thicket shrubs. Ten 30-meter lines were sampled per stand. Bare ground and litter intercepts were not recorded; these were left for inclusion in quadrat herbaceous plant sampling.

A 2-dm-by-5-dm quadrat supported on legs and made from small welding rods was used for herbaceous plant sampling. Sides of the quadrat were painted alternating colors at 1 dm intervals for ease in estimating percentage cover. Fifty quadrats were sampled per stand at 10-step intervals. Bare ground and litter estimates were obtained for the entire stand by this method.

From all data, calculations of absolute and relative density, absolute and relative dominance, and absolute and relative frequency were made with a final summation of relative values to yield importance value.

Soil characteristics were evaluated in several ways on the 10 sites chosen for intensive study. To determine soil physical characteristics, 100 samples per stand were taken at 10-step intervals with a steel rod penetrometer and penetration depth was recorded to the nearest decimeter. Physical characteristics of the gravel on gravel bars occupied by pioneer forest stands were determined by taking three to five samples with a shovel, screening each sample with a sieve of 0.5 by 0.5 cm with square-hole design, and calculating percentage rock and percentage sand, sand being all particles passing through the sieve mesh. Comparative samples were also taken from sites occupied by sandbar willow.

Five soil samples per site were collected in plastic bags at (1) surface on pioneer community gravel bar, (2) surface in mature forest, (3) 2 dm depth in mature forest, (4) surface on adjacent fescue prairie grassland, and (5) 2 dm depth on fescue prairie grassland. All rocks greater than 0.5 cm in diameter were removed from the samples. These samples were analyzed in the soils laboratory of the

Brigham Young University Department of Botany and Range Sciences for percentage sand, percentage silt, percentage clay, type, pH, and parts per million soluble salts following the directions of Bouyoucos (1936).

To determine average age of trees in a stand as well as the age of the oldest-appearing trees, samples were taken with a 46 cm increment borer and the corings were stored in glass tubing until rings could be counted in the laboratory. So many of the trees cored had heart rot (about 40 percent) that much of the coring was unproductive. However, sufficient growth ring information was obtained to justify the construction of aging formulae for tree species. These formulae were based on the average number of annual growth rings per centimeter of xylem and the tree trunk diameter at breast height.

Valley profiles were developed for each of the 10 major study sites utilizing a hand-held 30-meter steel tape, optical range finder, and pacing estimates. From these profiles the fraction of the river valley occupied by riverbottom forest was derived, plus forest height above stream level and terrace arrangement.

General observations and photographic work were carried out during all seasons of the years 1970 through 1973. Important phenological dates were recorded to yield seasonal development trends. The effects of stream flooding were noted with special attention to poplar seedling submergence and survival, channel alteration, silt deposition, mature forest destruction by erosion, and gravel bar formation.

Historical data on river changes and forest evolution and use were obtained through correspondence and interviews as well as library sources. General observations on bird and mammal life were also made thoughout the study years.

Results

General Features of River Valleys and Riverbottom Forest

Typical riverbottom forest begins on St. Mary River 3.2 km south of the international boundary where the river abruptly leaves the aspen parkland-fescue prairie transition and winds through the fescue prairie portion of the grassland biome. Riverbottom forest is continuous along 48 river km to St. Mary Reservoir except for one short discontinuity at the mouth of Coalmine Coulee. Below St. Mary Reservoir riverbottom forest is lacking for the 80 river km to the river's confluence at Lethbridge. The lack of riverbottom forest on St. Mary River coincides with river channel restraints imposed by the Bearpaw Shale formation. Streamfall along the river length averages 3.4 m per km. Where glacial and/or alluvial gravel deposits occur, riverbottom forest has developed.

On Lee Creek, riverbottom forest begins 1.6 km above the hamlet of Beazer. It is continuous for 20 stream km to the mouth of Lee Creek below Cardston. Riverbottom forest development is coincident with gravel bar formation. Streamfall averages 0.75 m per km.

Riverbottom forest development begins on Belly River 1.6 km above the Highway 5 bridge. As with St. Mary River and Lee Creek, the transition forest changes abruptly to riverbottom forest which is continuous to the Belly River-Waterton River confluence at Standoff. Riverbottom forest development coincides with gravel bar formation for the 48 stream km. Streamfall averages 3.2 m per km.

The channel pattern of the three streams is similar. They are "meandering" streams in the definition of Neill and Galay (1967). The potential energy of moving water has given these streams the ability to carve channels to their present shape. The flow pattern obeys the laws of stream morphology described by Yang (1971). Riverbottom forest is found on streams that have not reached a final static equilibrium but are still in a state of dynamic equilibrium, continually adjusting to achieve an approximate balance between work done and load imposed. Streamflow is such that degradation and aggradation occur each year. The peak periods of channel alteration and gravel bar formation were found to coincide with peak streamflow in late May and early June. The inability of these streams to adjust widths in accordance with velocity has led to the alternate deposition of gravel bars, first on one side of the stream and then on the other wherever the water has had access to transportable gravels. Gravel deposits

alternating with degraded banks are characteristic of the meander pattern.

Pioneer stands of riverbottom forest were observed growing on gravel bar formations but never on sand bars. On nine such pioneer riverbottom forest sites the gravel, on which many small poplars 0.15 to 0.6 m tall were growing, consisted of 61.1 percent rocks greater than 0.5 cm in diameter and 38.9 percent of particles less than 0.5 cm in diameter, in other words, sand (Fig. 4). On sites occupied by small sandbar willows, 100 percent of each soil sample passed through the 0.5-cm mesh screen.

Depth of easy penetration by the penetrometer on gravel bars occupied by pioneer riverbottom forest ranged from 0.0 dm to 1.0 dm, the mean being 0.4 dm. Ten gravel bars were sampled, one at each major site, with 100 penetrometer readings per site.

Gravel bars formed by annual flooding

Fig. 4. Recently formed first terrace gravel bar on St. Mary River open to invasion by riverbottom forest tree, shrub, and herb species.

were available to forest invasion and development by late June. Successful invaders were able to cope with a few days of submergence during flooding each spring. In 1971, 1972, and 1973 average number of flooddays per year was four. These occurred with greatest frequency during late May and early June. The poplar species on pioneer riverbottom forest sites are well leafed out by the time annual flooding commences. Three pioneer riverbottom forest stands on gravel bars between site 3, Cardwell's Island, and site 4, Woolford Park on St. Mary River, were observed for flood damage effect on the poplar species in late spring of 1972. On each of the three sites poplar seedlings and saplings 0.15 to 0.6 m tall were numerous prior to flooding. There were also many herbaceous plants. All sites were subjected to over-site flooding for three days. After flood water subsidence the pioneer tree stands were intact on two of the three gravel bars. Seedlings were somewhat muddy and bent over; otherwise they appeared to be uninjured. One week later they were thriving. A shallow layer of silt and sand 0.6 to 1.2 cm in depth had been deposited over the original gravel by the flood water.

On the remaining gravel bar, largest of the three, not a trace of the former pioneer tree stand could be found. The flood water had been directed over this gravel bar, altering its shape completely. All plant life had been buried or washed away, leaving several hundred square meters of fresh new gravel bar ready for re-invasion and establishment of the riverbottom forest community.

Lee Creek and the St. Mary and Belly rivers are principally degrading streams with several different terrace levels. Riverbottom forest is confined to the narrow band of gravel of the first and second terraces. The first terrace or "first bottom" of Lindsay et al. (1961) is unstable from modern river cutting and deposition and endures partial or total annual flooding. It supports the pioneer stages of riverbottom forest. The second terrace or "second bottom" is inundated only by floods of unusual proportions, such as the one of 1964. This second terrace supports the climax riverbottom forest community.

Elevation increase from terrace to terrace was measured. From low water

level in the stream to mean level of the first terrace is 0.3 to 1.0 m. The second terrace is 0.9 to 1.5 m higher than the first, and the third and fourth terraces are 1.2 to 2.4 m higher than the second and third terraces. The third and subsequent terraces are occupied by the same fescue prairie grassland community that is climax on the surrounding rolling hills of southwestern Alberta.

At the 10 study sites, mature riverbottom forest occupied 17 to 50 percent of the rim-to-rim valley width. The average riverbottom forest occupancy of the rim-to-rim valley width was 32 percent.

No evidence was found of invasion of grassland terraces by tree species. Evidence was found in several locations of the invasion of the forest by grassland species, the invasion being accelerated by localized high intensity sheep grazing. Reproduction of tree species at high intensity grazing sites was nil.

Long unused river channels higher in elevation than the present river channel were devoid of forest development.

The longevity of riverbottom forest stands was investigated and found to be dependent on factors other than possible age attainment and reproduction of its species. Few forest stands were found where tree species had grown to maturity, died, were dying, or were being replaced by forest or grassland. Most stands showed evidence of destruction during some stage of development by the eroding action of water on the forest-supporting gravel bar. Trees and shrubs washed away during the course of lateral degradation were deposited on newer gravel bars or were lodged against other plants farther downstream. Some had been lodged for several years, were partly decayed, and had trapped sand, gravel, and river debris.

The abrasiveness of transported gravels was found to have been most effective in debarking woody stems and roots of transported plants and thus limiting their regeneration. Woody plant fragments were checked on gravel bars at each of the three study streams for regenerative growth following uprooting and transport by the water. No accurate count was kept, but the majority had not regenerated even following partial burial in gravel by flooding. All showed abrasion damage to the bark, smaller branches, and roots,

this damage being a direct function of streamflow velocity. Under ideal conditions, doubling the water velocity may increase abrasive power by four times (Flint et al. 1941).

The Climax Forest

Major emphasis was placed on the status of the climax riverbottom forest community occurring on St. Mary River, Lee Creek, and Belly River in southwest Alberta, Canada. Numerical analyses, using standard methods, were performed for the mature tree canopy, tree reproduction, clumped shrub understory, thicket shrub understory, and herbaceous understory.

Following the example of Rice (1965), dominants in strata categories with very few species were designated as those species having importance value of 75 or more, based on the maximum importance value possibility of 300. Average number of species per stand for the tree canopy stratum was three, for tree reproduction three, and for clumped shrubs three. Therefore, an importance value of not less than 75 designated stand dominants in these three strata.

Designation of dominants for remaining strata followed the reasoning that with more (or fewer) species the importance values expected of dominants would decrease (or increase) proportionately. Average number of species per stand for the thicket shrub stratum was 7.5. Applying the inverse proportion rule, a stand dominant would be so designated if it had an importance value of at least 30.

There was an average of 30 species per stand for the herbaceous plant stratum. The inverse proportion rule designates 7.5 as the least importance value for stand dominants.

Identification of plant species was based on collections made during the course of fieldwork. The 1971 growing season was largely devoted to learning field identification characters of herbaceous species not in flower at the time of data sampling. Tree species identification, based on Brayshaw (1965), in this study recognized narrowleaf cottonwood (*Populus angustifolia*), balsam poplar (*P. balsamifera*), and the hybrids between these two, called herein "AB hy-

TABLE 1. Summary of the mature tree stratum data from 10 riverbottom forest stands in southwestern Alberta.

Species	Trees/hect.	Rel. dens.	Rel. dom.	Rel. freq.	Imp. val.
Populus angustifolia	91.5	32.3	29.5	32.7	94.5
P. balsamifera	88.9	31.4	27.7	30.8	89.9
P. X balsamifera	96.9	34.2	41.9	34.7	110.8
P. tremuloides	5.4	1.9	0.5	1.3	3.7
Picea glauca	0.6	0.2	0.4	0.5	1.1
Total	283.4	100.0	100.0	100.0	300.0

TABLE 3. Summary of the clumped shrub data from 10 mature riverbottom forest stands in southwestern Alberta.

Species	Shrubs/hect.	Rel. dens.	Rel. dom.	Rel. freq.	Imp. val.
Betula occidentalis	79.6	52.1	72.0	47.7	171.8
Cornus stolonifera	44.2	28.9	16.0	27.2	72.1
Salix lutea	21.4	14.0	11.0	19.5	44.5
Salix bebbiana	3.8	2.5	0.5	2.7	5.7
Crataegus chrysocarpa	3.0	2.0	0.4	1.8	4.2
Salix amygdaloides	0.8	0.5	0.1	1.1	1.7
Total	152.8	100.0	100.0	100.0	300.0

brid" (*P. angustifolia X balsamifera*). *Populus trichocarpa*, long considered a species in its own right, has recently been designated by Brayshaw (1965) as *P. balsamifera* subsp. *trichocarpa*. Recognizing only one species of balsam poplar greatly simplified fieldwork inasmuch as the fruiting capsules necessary for the identification of *P. trichocarpa* as a species were produced infrequently.

Summary data for the mature tree stratum are presented in Table 1. Density is expressed as the number of trees per hectare, and relative dominance was derived from stem basal area and density.

Tree reproduction data for the 10 stands are summarized in Table 2. Tree reproduction included tree species individuals with a stem diameter at 1.4 m above ground of 5 cm or less. Relative dominance was derived from average sapling height and density.

Clumped shrub data for the 10 stands are summarized in Table 3. Relative dominance for clumped shrubs was derived from average canopy coverage area and density.

Thicket shrub data summaries for the 10 stands appear in Table 4. *Potentilla fruticosa* exhibits some characteristics of clumped shrubs, but because of its smallness and multiple stem habit it was included in thicket shrubs. The woody vines were also included.

Herbaceous stratum data for the 10 stands are summarized in Table 5 which includes only those species with status as stand dominants or community dominants.

Unoccupied space, that is, bare ground, rock, and litter, was estimated during

TABLE 2. Summary of the tree reproduction data from 10 stands of mature riverbottom forest in southwestern Alberta.

Species	Sapl./hect.	Rel. dens.	Rel. dom.	Rel. freq.	Imp. val.
Populus angustifolia	113.3	42.0	38.3	38.6	118.9
P. balsamifera	81.5	30.2	32.4	28.1	90.7
P. X balsamifera	65.0	24.1	25.2	29.8	79.1
P. tremuloides	9.2	3.4	3.9	3.1	10.4
Picea glauca	0.8	0.3	0.2	0.4	0.9
Total	269.8	100.0	100.0	100.0	300.0

TABLE 4. Summary of the thicket shrub data from 10 mature stands of riverbottom forest in southwestern Alberta.

Species	Rel. dens.	% cover	Rel. dom.	Rel. freq.	Imp. val.
Elaeagnus commutata	29.6	10.4	31.0	19.9	80.5
Symphoricarpos occidentalis	26.1	4.9	14.6	18.3	59.0
Rosa woodsii	20.4	5.9	17.6	17.3	55.3
Amelanchier alnifolia	9.0	2.4	7.2	14.7	30.9
Potentilla fruticosa	5.5	3.0	8.9	7.5	21.9
Arctostaphylos uva-ursi	3.0	2.9	8.7	5.4	17.1
Juniperus horizontalis	1.9	2.4	7.2	5.2	14.3
Prunus virginiana	2.1	0.6	1.8	5.9	9.8
Shepherdia canadensis	0.6	0.4	1.2	1.6	3.4
Shepherdia argentea	0.6	0.2	0.6	1.6	2.8
Salix interior	0.3	0.2	0.6	1.0	1.9
Juniperus communis	0.3	0.2	0.6	0.8	1.7
Clematis ligusticifolia	0.5	trace	trace	0.5	1.0
Rubus strigosus	0.1	trace	trace	0.3	0.4
Total	100.0	33.5	100.0	100.0	300.0

TABLE 5. Summary of herbaceous species stand dominants based on a minimum importance value of 7.5 or more in at least 1 of the 10 stands. Community dominants, designated "CD" in the table, have an average importance value of not less than 7.5 and are dominant in at least 4 of the 10 stands.

Species	Avg. imp val.	No. stands dominant	Comm. dom.
Poa pratensis	41.9	8	CD
Medicago lupulina	26.3	6	CD
Poa compressa	12.1	5	CD
Chrysopsis villosa	11.1	5	CD
Solidago mollis	10.6	5	CD
Phleum pratense	10.4	5	CD
Oxytropis viscida	10.1	6	CD
Aster laevis	9.3	5	CD
Fragaria virginiana	7.5	4	CD
Bromus inermis	8.1	1	
Taraxacum officinale	6.7	5	
Stipa columbiana	6.6	2	
Poa secunda	5.6	5	
Agrostis alba	4.5	3	
Erigeron compositus	4.2	3	
Agropyron inerme	4.1	1	
Monarda fistulosa	4.1	3	
Achillea millefolium	4.0	3	
Agropyron trachycaulum	3.5	2	
Smilacina stellata	3.3	2	
Agropyron smithii	3.2	2	
Thlaspi arvense	3.1	2	
Zizia aptera	3.0	1	
Artemisia campestris	2.8	2	
Thermopsis rhombifolia	2.7	3	
Viola adunca	2.7	3	
Glycyrrhiza lepidota	2.4	2	
Galium boreale	2.4	2	
Melilotus officinalis	2.4	2	
Cirsium arvense	1.9	1	
Potentilla hippiana	1.8	1	
Petalostemon candidum	1.7	1	
Selaginella densa	1.7	1	
Lupinus argenteus	1.6	1	
Antennaria rosea	1.5	1	
Senecio canus	1.4	1	
Medicago sativa	1.2	1	
Linaria vulgaris	1.1	1	
Artemisia biennis	1.1	1	
Bupleurum americanum	1.0	1	
Vicia americana	1.0	1	
Penstemon nitidus	0.9	1	
Lathyrus ochroleucus	0.9	1	
Chrysanthemum leucanthemum	0.9	1	
Trifolium repens	0.9	1	
Anemone multifida	0.8	1	
Solidago gigantea	0.8	1	

herbaceous species sampling. Unoccupied space at this stratum ranged from 79.3 percent at Hillspring Park to 50.6 percent

at Highway 5 bridge; the average of all stands was 66.2 percent.

All calculations of community values were based on the equations of Cox (1967).

Using the formula $C = \dfrac{2w}{a + b}$, calculations of coefficient of community were made between all stands using all strata. Similarity values were totaled for all stands and dissimilarity values calculated on the basis of a maximum similarity coefficient between two stands of 85 (Cox 1967).

Comparison of coefficients of community and similarity and dissimilarity totals indicated that basic similarities within the 10 stands outweighed dissimilarities. These 10 stands were therefore deemed to be parts of the same riverbottom forest community. Pursuant to this, to typify the riverbottom forest community on the three streams, characteristics of typical riverbottom forest dominants were derived from the individual stand dominance values based on importance value, plus a somewhat arbitrary judgment that a community dominant must also be a stand dominant in no fewer than 4 of the 10 stands.

In the riverbottom forest of Lee Creek, St. Mary, and Belly rivers the most important mature tree was the AB hybrid poplar (*Populus* x *balsamifera*), a dominant in 9 of the 10 stands and with the highest average importance value for tree species, 110.8. A close second was narrowleaf cottonwood (*P. angustifolia*), a dominant in 9 of the 10 stands and with an average importance value of 94.5. Third was balsam poplar (*P. balsamifera*), a dominant in 7 of the 10 stands and with an average importance value of 89.9. These three trees, a hybrid and its two parent species, identify the tree canopy stratum of the riverbottom forest community on these three streams. Quaking aspen (*P. tremuloides*) and white spruce (*Picea glauca*) are relatively unimportant species in spite of their very high importance in the aspen parkland and montane forest biomes nearby. No distinctive trends or patterns were noted in dominant species change from upstream to downstream stands.

For the tree reproduction stratum within the climax forest stands similar results were obtained. The most impor-

tant species was narrowleaf cottonwood, a dominant in 8 of 10 stands with an average importance value of 118.9. Balsam poplar was second, a dominant in 6 of 10 stands, with an average importance value of 90.7. Third was the AB hybrid poplar, a dominant in 6 of 10 stands, with an average importance value of 79.1. The three dominant species in the tree reproduction stratum are the same as the dominant species in the mature forest tree stratum with closely grouped average importance values and stand-dominant values.

The minor tree species, quaking aspen, and white spruce, were also the minor species in the tree reproduction stratum.

Absolute density of tree species ranged from a low density of 122.6 trees per hectare at site 1, Cook's Ranch, to a high density of 517.8 trees per hectare at site 7, Highway 5 bridge. Average density of all stands was 283.4 trees per hectare.

Of the six species of clumped shrubs encountered in sampling, only two occurred in 4 or more of the 10 stands and none in 10 of 10. River birch (*Betula occidentalis*) was the number one dominant clumped shrub for the riverbottom forest community of this study. It occurred as a dominant in 9 of the 10 stands and had an average importance value of 171.8. The other community dominant was redosier dogwood (*Cornus stolonifera*), a dominant in 7 of 10 stands and with an average importance value of 72.1. Yellow willow (*Salix lutea*) was a dominant in 3 of 10 stands, but its average importance value of 44.5 was too low for consideration as a community dominant.

Of the 14 species of thicket shrubs encountered in sampling, 8 were dominants in at least 1 stand. Only 4 were judged community dominants. First was silverberry (*Elaeagnus commutata*), a dominant in 8 of 10 stands and with an average importance value of 80.5. Second was snowberry (*Symphoricarpos occidentalis*) occurring in 8 of 10 stands as a dominant and with an average importance value of 59.0. Third was wood rose (*Rosa woodsii*), dominant in 7 of 10 stands, average importance value 55.3. Fourth was serviceberry (*Amelanchier alnifolia*), a dominant in 4 of 10 stands and with an average importance value of 30.9.

Nine community dominants were found among the herbaceous species in the 10 stands. Forty-nine species were dominants in at least one stand. The community dominants in descending order followed by frequency of dominance and average importance value are: *Poa pratensis*, 8 of 10, 41.9; *Medicago lupulina*, 6 of 10, 26.3; *Poa compressa*, 5 of 10, 12.1; *Chrysopsis villosa*, 5 of 10, 11.1; *Solidago mollis*, 5 of 10, 10.6; *Phleum pratense*, 5 of 10, 10.4; *Oxytropis viscida*, 6 of 10, 10.1; *Aster laevis*, 5 of 10, 9.3; and *Fragaria virginiana*, 4 of 10, 7.5.

All of the dominant tree and shrub species are native to Alberta. Five of the herbaceous species community dominants are native and four are exotics.

Penetrometer readings throughout the forest stands tended to reflect the sand and silt deposition brought about by earlier overbank flooding. The litter layer, even under the highest density forest at site 7, Highway 5 bridge (517.8 trees per hectare), did not exceed 5 cm. The minimum penetrometer reading at most stands was 0.0 dm, and maximum readings of 9.0 dm were not uncommon. Mean penetration of soil under mature forest was 2.5 dm, in considerable contrast to the 0.4 dm mean obtained from pioneer gravel bar sites.

The pH of gravel bar soil was very close to 8.0 at all sites, with a moderation toward a slightly less alkaline reaction in the forest sites where pH values averaged 7.6 at the surface and 7.8 at a depth of 2 dm. Neighboring grassland soils on terrace three were more moderate yet with an average surface pH of 7.5 and a 2-dm-depth pH of 7.7. A decrease in sand and an increase in silt and clay fractions occurred from gravel bar to forest to grassland, these data complementing penetrometer data. Parts per million of soluble salts increased markedly, from the gravel bar surface average of 176 ppm, to 458 ppm in forest surface soils, to 409 ppm in grassland surface soils. No analyses were undertaken for organic carbon, total nitrogen, or total phosphorus.

An age determination formula was devised to facilitate approximating average tree age and age of the largest tree in each stand. The basic formula was: Age in years $= \dfrac{(d - bd)}{2}$ $r+5$; where *d* equals

the diameter in centimeters of the tree trunk at 1.4 m above ground, b equals the fraction of the diameter that is bark, r the average number of annual rings per centimeter of xylem, and "plus 5" is an approximation of the number of years the tree took to reach a height of 1.4 meters. Values for b and r were constructed through the use of an increment borer, with no fewer than 20 samples being taken for each tree species throughout the range of the 10 study sites. For narrowleaf cottonwood b equals 0.2 and r equals 3.74; for balsam poplar b equals 0.184 and r equals 3.70; for the AB hybrid poplar b equals 0.193 and r equals 3.78; and for quaking aspen b equals 0.073 and r equals 5.5. Values for b and r were not determined for white spruce. Bark thickness for the AB hybrid poplar was intermediate between those of its parent species and growth rate of the AB hybrid was slowest of the three.

Smallest average diameter and lowest average age species was narrowleaf cottonwood with an average diameter of 20.8 cm and average age of 36 years for all stands. Second oldest species was balsam poplar with an average diameter of 21.8 cm and average age of 38 years. The AB hybrid poplar had the largest average diameter, 26.2 cm, and the highest average age, 45 years.

Narrowleaf cottonwood was the largest tree sampled in two stands. Largest diameters of 36 and 43 cm for this species were found in two stands. Corresponding ages were 58 and 69 years. Balsam poplar was the largest tree sampled in one stand. This tree, 48 cm in diameter, was 78 years old. The AB hybrid poplar was the largest tree sampled in eight stands. The average diameter of these large poplars was 53 cm and average age 85 years. The largest tree in any sample, an AB hybrid, was 89 cm in diameter with an age of 141 years. The average age of the largest trees sampled in the stands was 40 years.

A search was conducted on each of the three streams for very large and, presumably, very old trees. These would provide some indication of the possible age attainment of dominant tree species. Through actual increment boring the oldest tree found was an AB hybrid poplar on Lee Creek three miles below Beazer that was, in 1973, 250 years old.

Another large AB hybrid, with a diameter of 129 cm and approximate age of 200 years, was found at the Kearl Ranch on Lee Creek three miles southwest of Cardston. Other large trees in Kearl's private picnic ground were a narrowleaf cottonwood 160 years old and a balsam poplar 100 years old.

The largest tree found on St. Mary River, near Woolford Park, was an AB hybrid poplar with a 102 cm diameter at 1.4 m above ground and an approximate age of 160 years. Nearby was a balsam poplar 97 cm in diameter and approximately 155 years old.

Height of the large trees ranged from 13 to 22 m. At no site were trees tall enough to project much above the valley rim.

First leaf-out of tree species began at site 10, Standoff, on 13 May 1972. One week later tree leaf-out was beginning on the upper St. Mary River at site 2, east of Aetna, on Lee Creek at site 5, Town Dam, and at site 8, Hillspring Park on Belly River.

Leaf-out was not simultaneous at any one site for all poplar species. For example, on 14 May 1972 balsam poplar and prevernal aspen were leafing out at site 10, Standoff. By 18 May the same species were beginning leaf-out at site 4, Woolford Park. The AB hybrids were just beginning leaf-out at site 10, Standoff, on 21 May and at site 4, Woolford Park, on 28 May. By 21 May narrowleaf cottonwoods were leafing out at site 10, Standoff, but had not yet begun to do so at site 4, Woolford Park, nor at any sites upstream from there. Leaf-out sequence of community tree dominants at any given site is first, balsam poplar; second, the AB hybrids; and third, narrowleaf cottonwood.

The shrub species followed a leaf-out sequence that began, in 1972, on 21 May at site 10, Standoff, and worked from there upstream and toward the mountains on all stream sites. Woody plant leaf-out progressed upstream at the rate of five river kilometers per day under mild weather conditions.

The importance of riverbottom forest to man in the early days of the Canadian west was variable. Certainly use of the forest for shelter and firewood was made by aboriginal man. Prior to 1877 this part of the northern great plains was

controlled by Indian tribes of the Blackfeet Confederacy. Ewers (1958) reported that Indian use of riverbottom forest was principally limited to winter season encampments. Ewers also reported the feeding of the inner bark of cottonwood trees to horses when snow was too deep for grassland feeding.

Walter McClintock (1910), who lived with the Blackfeet Indians from 1896 to 1900, wrote that the Indian name for St. Mary River meant "Green Banks" because of its gallery forests of poplars. He also reported riding through groves of large cottonwoods along the Belly River.

Between 1870 and 1900 many settlers arrived from eastern Canada and United States to take up homesteads offered by the Canadian government. Since many of these people came from forested regions, to feel more at home they settled in the river valleys, occasionally in the riverbottom forest itself.

The town of Cardston, founded in 1887 by Charles Ora Card from Cache Valley in Utah, was built in part of the riverbottom forest of Lee Creek. Photographs taken of Cardston during the period 1887 to 1900 show the riverbottom forest in much the same position and with the same general appearance as today (Macleod 1900). Major floods of 1889, 1903, and 1964 taught the residents about the hazards of living in riverbottom forest.

Settlers in southwestern Alberta reported that cottonwood logs made poor building material, being crooked and subject to early decay. Lumber of quality could not be cut from them. Cottonwood made poor firewood; the logs tended to smoulder rather than burn and smaller branches burned too quickly. Building logs, lumber, and shingles came from the forests of spruce and pine on lower mountain slopes 20 miles to the southwest. Coal was found in abundance, further reducing the need for trees as fuel (Hudson 1963). A cottonwood log cabin built in 1885 on Lee Creek by E. N. Barker has long since rotted away with no trace of its logs remaining. Cabins built of pine and spruce logs at the same time still stand (Barker 1937).

In 1896 Collector of Customs Frederick D. Shaw, an immigrant from wooded Nova Scotia, built his beautiful home "Woodgrove Park" in a mature stand of riverbottom forest on a second terrace of St. Mary River east of Cardston. Within 10 years the home had to be abandoned and was ultimately destroyed by the river, which had initially seemed far enough away for safety (P. C. Shaw pers. comm.).

My grandfather, Vernon S. Shaw, remarked in the early 1950s that the huge (AB hybrid) cottonwood at the Kearl Ranch on Lee Creek seemed just as large to him when he was a boy in 1885 as it did at present. This tree, estimated to be 200 years old in 1973, would have been about 114 years old in 1885 and a very large tree even then.

Today, of 13 ranch homes in Lee Creek valley, only 1 is built in riverbottom forest on a second terrace, and that one is protected from flood damage by a road serving as a dike. Of the 14 ranch homes on St. Mary River between the international boundary and St. Mary Reservoir, not 1 is built in riverbottom forest. Along Belly River 3 out of 10 ranch homes and several homes on the Blood Indian Reservation at Standoff are in riverbottom forest and are annually in danger of flood damage.

During the years from 1950 to 1970 provincial and municipal boards established picnic and camp grounds at four riverbottom forest sites. On St. Mary River parks were established at Kimball and Woolford, on Belly River at a site near Hillspring, and on Lee Creek at Cardston. Woolford Park has been subjected to frequent and serious flood damage with over half of the original acreage on the second terrace lost to river erosion in spite of attempts made to divert the river. Streambank stabilization using broken concrete slabs has been necessary at the Cardston park to prevent erosional loss. Hillspring Park is protected from flood damage by the United Irrigation District diversion dam.

Preservation of intact riverbottom forest has been fortuitous.

Throughout the years of this study, 1970 to 1973, observations of a general nature were made on common bird and mammal species of the riverbottom forest. The most frequently sighted birds, in the order in which they appear in Salt and Wilk (1958), were: great blue heron, red-tailed hawk, killdeer, spotted sandpiper, California gull, ring-billed gull,

mourning dove, great horned owl, common nighthawk, kingfisher, red-shafted flicker, black-billed magpie, common crow, house wren, catbird, robin, starling, yellow warbler, house sparrow, and American goldfinch. The black-billed magpie is the most typical bird of the riverbottom forest.

The most frequently sighted native mammals, in the order in which they appear in Soper (1964), were: white-tailed prairie hare, American varying hare, Black Hills cottontail rabbit, pale-striped ground squirrel, buff-bellied chipmunk, Canada beaver, white-footed mouse, meadow vole, jumping mouse, porcupine, northern plains skunk, mule deer, and white-tailed deer.

Taxonomic Treatment

Vascular plants were collected at the 10 major study sites and at 9 minor sites on St. Mary River, Lee Creek, and Belly River during the growing seasons of 1970, 1971, 1972, and 1973. Plants included as riverbottom forest species were collected from pioneer forest sites on gravel bars and from the riverbottom forest-fescue prairie grassland transition as well as from the area of major interest, the mature riverbottom forest.

The southwestern Alberta riverbottom forest community contained 291 species of vascular plants in 165 genera representing 50 plant families. Of these, 41 are woody plant species and the remaining 250 are herbaceous plant species.

The most important plant families represented were: Compositae, 30 genera, 61 species; Leguminosae, 12 genera, 39 species; Gramineae, 16 genera, 28 species; Rosaceae, 8 genera, 16 species; Salicaceae, 2 genera, 13 species or species hybrids; and Umbelliferae, 8 genera, 12 species.

One species new to the province of Alberta was found. *Prunus nigra* Ait. was collected in 1971 from a small population on Lee Creek at site 6, Slaughter Hole (Shaw 1218). In earlier editions of Native Trees of Canada (1949, 1956, 1961), Canada Plum (*Prunus nigra*) was reported from New Brunswick west into Manitoba. It was also reported from ". . . fords of several rivers in southern Alberta." The seventh edition (Hosie 1969) made no mention of the Alberta report. This, according to T. C. Brayshaw

(pers. comm.), was deleted because no specimens could be found to substantiate the report. This report of *Prunus nigra* in southwestern Alberta is now verified (Cody and Shaw 1973).

Range extensions for 12 species were obtained from the collection data of this study, these being noted in the species list.

Species List

POLYPODIACEAE
Cystopteris fragilis (L.) Bernh.

EQUISETACEAE
Equisetum laevigatum A. Br.
Equisetum pratense Ehrh.

SELAGINELLACEAE
Selaginella densa Rydb.

PINACEAE
Juniperus communis L.
Juniperus horizontalis Moench
Juniperus scopulorum Sarg. (Range extension)
Picea glauca (Moench) Voss var.
    albertiana (S. Brown) Sarg.
Pinus flexilis James
Pseudotsuga menziesii (Mirb.) Franco

TYPHACEAE
Typha latifolia L.

ALISMACEAE
Sagittaria cuneata Sheld.

GRAMINEAE
Agropyron dasystachyum (Hook.) Scribn.
Agropyron inerme (Scribn. & Smith) Rydb.
Agropyron smithii Rydb.
Agropyron smithii Rydb. var.
    molle (Scribn. & Smith) Jones
Agropyron subsecundum (Link) Hitchc.
Agropyron trachycaulum (Link) Malte
Agrostis alba L.
Agrostis variabilis Rydb.
Beckmannia syzigachne (Steud.) Fern.
Bouteloua gracilis (HBK.) Lag.
Bromus ciliatus L.
Bromus inermis Leyss.
Bromus tectorum L.
Calamagrostis inexpansa A. Gray
Dactylis glomerata L.
Deschampsia caespitosa (L.) Beauv.
Deschampsia caespitosa (L.) Beauv. var.
    glauca (Hartm.) Sam.
Elymus cinereus Scribn. & Merr.
Elymus glaucus Buckl.
Glyceria borealis (Nash) Batchelder
Glyceria grandis S. Wats.
Koeleria cristata (L.) Pers.
Oryzopsis hymenoides (R. & S.) Ricker
Phalaris arundinacea L.
Phleum pratense L.
Poa compressa L.
Poa cusickii Vasey
Poa interior Rydb.
Poa pratensis L.
Stipa columbiana Macoun

CYPERACEAE
Carex flava L.
Eleocharis palustris (L.) R. & S.
Scirpus acutus Muhl.
Scirpus paludosus A. Nels.

JUNCACEAE
Juncus alpinus Vill. var. *rariflorus* Hartm.
Juncus longistylis Torr.
Juncus torreyi Coville

LILIACEAE
Allium cernuum Roth
Allium schoenoprasum L. var.
  sibiricum (L.) Hartm.
Allium textile Nels. & Macbr.
Disporum oreganum (A. Wats.) B. & H.
Fritillaria pudica (Pursh) Spreng.
Lilium philadelphicum L. var.
  andinum (Nutt.) Ker
Smilacina racemosa (L.) Desf. var.
  amplexicaulis (Nutt.) S. Wats.
Smilacina stellata (L.) Desf.
Zygadenus gramineus Rydb.

IRIDACEAE
Sisyrinchium montanum Greene

ORCHIDACEAE
Calypso bulbosa (L.) Oakes (Range extension)
Corallorhiza striata Lindl.
Habenaria hyperborea (L.) R. Br.
Habenaria viridis (L.) R. Br. var.
  bracteata (Muhl.) A. Gray

SALICACEAE
Populus acuminata Rydb.
Populus angustifolia James
Populus angustifolia James X *balsamifera* L.
Populus balsamifera L. subsp.
  trichocarpa (T. & G.) Brayshaw
Populus sargentii Dode
Populus tremuloides Michx.
Salix amygdaloides Anderss.
Salix bebbiana Sarg.
Salix caudata (Nutt.) Heller
Salix interior Rowlee
Salix lutea Nutt.
Salix petiolaris J. E. Sm.
Salix scouleriana Barratt

BETULACEAE
Betula occidentalis Hook.

URTICACEAE
Urtica lyallii S. Wats. (Range extension)

SANTALACEAE
Comandra pallida A. DC.

POLYGONACEAE
Eriogonum flavum Nutt.
Rumex crispus L.
Rumex mexicanus Meisn.

CARYOPHYLLACEAE
Arenaria lateriflora Poir.
Cerastium arvense L.

RANUNCULACEAE
Actaea rubra (Ait.) Willd.
Actaea rubra (Ait.) Willd. forma
  neglecta (Gillman) Robins.
Anemone multifida Poir.
Clematis ligusticifolia Nutt.

Clematis verticellaris DC. var.
  columbiana (Nutt.) A. Gray
Ranunculus acris L.
Ranunculus cymbalaria Pursh
Ranunculus pedatifidus J. E. Smith var.
  affinis (R. Br.) L. Benson
Ranunculus repens L. (Range extension)
Thalictrum venulosum Trel.

CAPPARIDACEAE
Cleome serrulata Pursh

CRUCIFERAE
Arabis hirsuta (L.) Scop. var.
  glabrata T. & G.
Arabis holboellii Hornem.
Arabis holboellii Hornem var.
  retrofracta (Graham) Rydb.
Draba aurea Vahl (Range extension)
Erysimum cheiranthoides L.
Lesquerella alpina (Nutt.) S. Wats. var.
  spathulata (Rydb.) Payson
Lesquerella arenosa (Richards.) Rydb.
Physaria didymocarpa (Hook.) A. Gray
Sisymbrium loeselii L.
Thlaspi arvense L.

CRASSULACEAE
Sedum stenopetalum Pursh

SAXIFRAGACEAE
Parnassia palustris L. var. *neogaea* Fern.
Ribes inerme Rydb. (Range extension)
Ribes oxyacanthoides L.

ROSACEAE
Amelanchier alnifolia Nutt.
Chamaerhodos erecta (L.) Bunge ssp.
  nuttallii (Pickering) Hulten
Crataegus chrysocarpa Ashe
Fragaria virginiana Duchesne var.
  glauca S. Wats.
Fragaria virginiana Duchesne var.
  platypetala (Rydb.) Hall
  (Range extension)
Potentilla anserina L.
Potentilla concinna Richards.
Potentilla fruticosa L.
Potentilla gracilis Dougl.
Potentilla hippiana Lehm.
Prunus nigra Ait.
  (New record for Alberta)
Prunus virginiana L. var.
  melanocarpa (A. Nels.) Sarg.
Rosa acicularis Lindl.
Rosa woodsii Lindl.
Rubus strigosus Michx.

LEGUMINOSAE
Astragalus aboriginum Richards.
Astragalus adsurgens Pall. ssp.
  robustior (Hook.) Welsh
Astragalus agrestis Dougl.
Astragalus alpinus L.
Astragalus bisulcatus (Hook.) A. Gray
Astragalus bourgovii A. Gray
  (Range extension)
Astragalus canadensis L.
Astragalus crassicarpus Nutt. var.
  paysoni (Kelso) Barneby
Astragalus drummondii Dougl.
Astragalus flexuosus Dougl.
Astragalus miser Dougl. var.
  serotinus (Gray) Barneby

Astragalus missouriensis Nutt.
Astragalus robinsii A. Gray var.
    minor (Hook.) Barneby
Astragalus tenellus Pursh
Astragalus vexilliflexus Sheld.
Glycyrrhiza lepidota Pursh
Hedysarum alpinum L. var.
    americanum Michx.
Hedysarum boreale Nutt.
Hedysarum sulphurescens Rydb.
Lathyrus ochroleucus Hook.
Lathyrus venosus Muhl. var.
    intonsus Butters & St. John
Lupinus argenteus Pursh
Lupinus sericeus Pursh
Medicago falcata L.
Medicago lupulina L.
Medicago sativa L.
Melilotus alba Desr.
Melilotus officinalis (L.) Lam.
Oxytropis campestris (L.) DC. var.
    gracilis (A. Nels.) Barneby
Oxytropis sericea Nutt. var.
    spicata (Hook.) Barneby
Oxytropis splendens Dougl.
Oxytropis viscida Nutt.
Petalostemon candidum (Willd.) Michx.
Petalostemon purpureum (Vent.) Rydb.
Thermopsis rhombifolia (Nutt.) Richards.
Trifolium hybridum L.
Trifolium pratense L.
Vicia americana Muhl.
Vicia sparsifolia Nutt.

GERANIACEAE
Geranium richardsonii Fisch. & Trauty.
Geranium viscosissimum Fisch. & Mey.

LINACEAE
Linum lewisii Pursh

EUPHORBIACEAE
Euphorbia esula L.

ANACARDIACEAE
Rhus trilobata Nutt.

ACERACEAE
Acer negundo L. var.
    interius (Britt.) Sarg.

MALVACEAE
Sphaeralcea coccinea (Pursh) Rydb.

VIOLACEAE
Viola adunca J. E. Smith
Viola rugulosa Greene

LOASACEAE
Mentzelia decapetala (Pursh) Urban & Gilg

ELAEAGNACEAE
Elaeagnus commutata Bernh.
Shepherdia argentea Nutt.
Shepherdia canadensis (L.) Nutt.

ONAGRACEAE
Epilobium angustifolium L.
Epilobium glandulosum Lehm.
Epilobium latifolium L.
Gaura coccinea Pursh
Gaura coccinea Pursh var.
    glabra (Lehm.) Torr. & Gray

Oenothera biennis L. var.
    hirsutissima Gray
Oenothera caespitosa Nutt.

UMBELLIFERAE
Bupleurum americanum Coult. & Rose
Cicuta douglasii (DC.) Coult. & Rose
Heracleum lanatum Michx.
Lomatium dissectum (Nutt.) Mathias
    & Constance var. multifidum (Nutt.) M. & C.
Lomatium foeniculaceum (Nutt.)
    Coult. & Rose
Lomatium simplex (Nutt.) Macbr. var.
    leptophyllum (Hook.) Mathias
Osmorhiza depauperata Philippi
Osmorhiza longistylis (Torr.) DC.
Osmorhiza occidentalis (Nutt.) Torr.
Perideridia gairdneri (Hook. & Arn.) Mathias
Sanicula marilandica L.

CORNACEAE
Cornus stolonifera Michx.

PYROLACEAE
Pyrola asarifolia Michx.
Pyrola asarifolia Michx. var.
    purpurea (Bunge) Fern.

ERICACEAE
Arctostaphylos uva-ursi (L.) Spreng.

PRIMULACEAE
Androsace septentrionalis L. var.
    subumbellata A. Nels.
Lysimachia ciliata L.

GENTIANACEAE
Gentiana affinis Griseb.
Gentianella amarella (L.) Borner ssp.
    acuta (Michx.) J. M. Gillett

APOCYNACEAE
Apocynum cannabinum L.

POLEMONIACEAE
Phlox hoodii Richards.
Polemonium pulcherrimum Hook.

BORAGINACEAE
Cryptantha celosioides (Eastw.) Payson
Cynoglossum officinale L.
Hackelia americana (A. Gray) Fern.
    (Range extension)
Hackelia floribunda (Lehm.) I. M. Johnston
Lappula echinata Gilib.
Lithospermum incisum Lehm.
Lithospermum ruderale Lehm.
Onosmodium occidentale Mackenzie

LABIATAE
Galeopsis tetrahit L.
Mentha arvensis L. var. villosa
    (Benth.) S. R. Stewart
Monarda fistulosa L. var.
    menthaefolia (Graham) Fern.
Prunella vulgaris L.

SCROPHULARIACEAE
Castilleja miniata Dougl.
Castilleja septentrionalis Lindl.
Linaria vulgaris Hill
Orthocarpus luteus Nutt.
Penstemon confertus Dougl.
Penstemon nitidus Dougl.

Penstemon procerus Dougl.
Rhinanthus crista-galli L.
Verbascum thapsus L.

RUBIACEAE
Galium aparine L. var.
　echinospermum (Wallr.) Farwell
Galium boreale L.

CAPRIFOLIACEAE
Lonicera dioica L. var.
　glaucescens (Rydb.) Butters
Lonicera involucrata (Richards.) Banks.
Lonicera tartarica L.
Symphoricarpos occidentalis Hook.

CAMPANULACEAE
Campanula rotundifolia L.

COMPOSITAE
Achillea millefolium L. var.
　lanulosa (Nutt.) Piper
Agoseris glauca (Pursh) Raf.
Antennaria rosea Greene
Arctium minus (Hill) Bernh.
Arnica cordifolia Hook.
Arnica fulgens Pursh
Aster ciliolatus Lindl.
Aster laevis L. var. *geyeri* A. Gray
Aster occidentalis (Nutt.) T. & G.
Aster pansus (Blake) Cronq.
Artemisia biennis Willd.
Artemisia campestris L. ssp.
　caudata (Michx.) H. & G.
Artemisia longifolia Nutt.
Artemisia ludoviciana Nutt.
Balsamorhiza sagittata (Pursh) Nutt.
Chrysanthemum leucanthemum L.
Chrysopsis villosa (Pursh) Nutt. var.
　hispida (Hook.) Gray
Crepis intermedia A. Gray
Cirsium arvense (L.) Scop.
Cirsium undulatum (Nutt.) Spreng.
Cirsium vulgare (Savi) Airy-Shaw
Erigeron acris L.
Erigeron caespitosus Nutt.
Erigeron compositus Pursh var. *glabrata* Macoun
Erigeron glabellus Nutt. var.
　pubescens (Hook.) Cronq.
Erigeron peregrinus (Pursh) Greene ssp.
　callianthemus (Greene) Cronq.
　(Range extension)
Erigeron philadelphicus L.
Erigeron speciosus (Lindl.) DC.
　(Range extension)
Erigeron strigosus Muhl.
Gaillardia aristata Pursh
Grindelia squarrosa (Pursh) Dunal var.
　quasiperennis Lunell
Gutierrezia sarothrae (Pursh) Britt. & Rusby
Helianthus annuus L. ssp.
　lenticularis (Dougl.) Cockerell
Helianthus laetiflorus Pers. var.
　subrhomboideus (Rydb.) Fern.
Helianthus nuttallii T. & G.
Hieracium canadense Michx.
Hieracium cynoglossoides Arv.-Touv.
Hieracium umbellatum L.
Hymenoxys acaulis (Pursh) Parker
Hymenoxys richardsonii (Hook.) Cockerell
Lactuca serriola L.
Liatris punctata Hook.

Lygodesmia juncea (Pursh) D. Don
Ratibida columnifera (Nutt.) Wooton
　& Standl.
Rudbeckia serotina Nutt.
Senecio canus Hook.
Senecio integerrimus Nutt. var.
　exaltatus (Nutt.) Cronq.
Senecio lugens Richards.
Senecio pauperculus Michx.
Solidago gigantea Ait.
Solidago graminifolia (L.) Salisb. var.
　major (Michx.) Fern.
Solidago missouriensis Nutt.
Solidago multiradiata Ait. (Range extension)
Solidago spathulata DC.
Sonchus asper (L.) Hill
Sonchus uliginosus Bieb.
Taraxacum officinale Weber
Townsendia parryi D.C. Eat.
Tragopogon dubius Scop.

DISCUSSION

The rather widely held belief that native cottonwood species have not populated the prairies of southwestern Alberta because of lack of shelter from the wind is open to closer scrutiny. Native poplar and cottonwood species have been successfully transplanted from natural riverbottom forest populations to prairie grassland sites. Furthermore, hybrid and exotic poplar species have been planted with excellent success on the prairies during the past 80 years. The barrier to native poplar invasion of the grasslands is partly a reproductive one. Mature trees in yard and shelterbelt plantings produce quantities of seed, but these observedly have failed to produce new plants. The seeds of native poplars are transported far and wide by the generous wind. If lack of shelter is the only factor responsible for the failure of poplar seedling survival, then there must surely be evidence of seed germination and partial seedling growth on some parts of the prairie grassland. No such evidence was found.

However, seeds from southwestern Alberta riverbottom forest poplar species will readily germinate and grow if they are provided with two essential environmental conditions in addition to the obvious ones of temperature, etc. First, there must be gravel beds or bars with a make-up of about 40 percent sand (particles less than 0.5 cm in diameter) and 60 percent rock; and, second, these gravel beds or bars must be water saturated to the surface at frequent intervals during the growing season, and there must be a

high water table, within 4 to 10 dm of the surface, at other times.

The necessity of the gravel being in streamside bars is not absolute since poplar seeds have readily germinated and developed into trees in abandoned high water table gravel pits on the prairies, for example, 1.5 km west of Fort Macleod and 1.5 km west of Cardston. These trees are poorly sheltered from the wind.

New gravel bars saturated with water on the streams of southwestern Alberta are quickly populated by seedlings of riverbottom forest poplar species. These are capable of developing into mature forest trees if the gravel bar or terrace remains intact.

High quality loam soil with high soil moisture will not produce forest growth. Such sites on the sheltered high banks of rivers and coulees may have tangled thickets of serviceberry, chokecherry, honeysuckle, and hawthorn but rarely are there poplars growing with them.

In southwestern Alberta, streams such as Rolph Creek, Snake Creek, and Boundary Creek, plus some sections of the north and south forks of Milk River, have high water tables in bankside sand-silt soils; yet they are without riverbottom forest. They are well within the survival and seed dissemination ranges of native poplars.

Gravel banks and perched ancient river valley terraces, with gravel in abundance, having subsurface drainage, are without riverbottom forest. River valley gravel bars formed by unusually high flood waters and left too high for subsurface water saturation will also fail to develop riverbottom forest stands. Herbaceous species may be quite successful on such sites, however.

Streams flowing in very shallow valleys, for example the Little Bow River, or in very open coulees like Pinepound Coulee are without riverbottom forest not entirely because of exposure to the wind but because the necessary high water table streamside gravels are not available.

Stream systems also provide excellent seed dispersal mechanisms. Flowing water will bring mountain or submontane species to greater range extensions down the valleys. Wind-borne seeds are readily dropped in the lee of sheltering banks and thickets where wind velocity decreases. Bird activities provide other transport mechanisms. Downstream species are able to extend their ranges upstream nearly as readily. In spite of its constancy of change, the riverbottom forest floodplain is a very uniform habitat where macroclimate and substrate definitely determine the establishment of plant species, where soil moisture conditions are less rigorous than in the uplands, and where the habitat can be quite uniform over wide geographical areas.

Riverbottom forest species are opportunists who take advantage of pioneer sites offered and survive for greater or lesser periods of time as successional trends and competition dictate. The number of plant species found in any stratum of the riverbottom forest community is a direct function of the number of species adapted to survive the climatic and soil regimes. There are many more species of herbaceous plants than woody ones on the northern great plains, and a pioneer site such as a gravel bar is a prime target for colonization by many more herbaceous species than woody ones. In this study the ratio of the riverbottom forest woody species to herbaceous species was 41 to 250.

Plant survival in the floodplain habitat is considered from the standpoints of survival of the individual and survival of the species. The woody perennials survive as individuals for periods of time as short as one growing season or as long as 250 years. Species populations survival is insured because only small portions of the total riverbottom forest community area are destroyed each year and the annual re-establishment of species on pioneer sites offsets population destruction.

The occurrence of many perennial forbs, as well as annuals, on pioneer gravel bar sites is probably due as much to reseeding each year as to renewed growth from perennating buds. This is true on the many first terrace sites where annual high water results in erosion of the substrate and consequent removal of most overwintering organs of herbaceous species, with the exception of more densely intertwined and matted root systems. Thus, abundant seed production is a principal species-survival mechanism, provided such seeds are not subject to

damage by water. Abundant seed production is a characteristic of members of the most important plant families represented on pioneer gravel bar sites: Compositae, Leguminosae, and Gramineae.

While survival of the species population is of primary significance in terms of the vegetation, in terms of mature riverbottom forest stands survival and life span of the individual are important. Hence, the successional trend from gravel bar pioneer site to mature riverbottom forest has, as its parallel, a trend from herbaceous annuals or short-lived herbaceous perennials with high seed production toward longer-lived woody species and herbaceous understory perennials.

The ephemeral nature of the riverbottom forest community is most favorable for establishment of any edaphically and climatically adapted species of plant capable of producing viable seed. Colonization of a new gravel bar by poplars may be dependent on the production and distribution of seed in the same year as gravel bar formation. Which poplar species or species hybrids dominate the early stages in riverbottom forest development may be a function of which of them produced the greatest or indeed any amount of seed during the year of colonization. Poplar species in southwestern Alberta do not flower and produce seed every year.

Seeds of the southwestern Alberta riverbottom forest community poplar dominants when produced are out of dehiscing capsules by mid-June to mid-July, just at the time when advantage can be taken of newly formed gravel bars, high water tables in gravels, and high precipitation rates. Survival is thus enhanced.

If poplars are to be successful in populating new gravel bars, they must be able to survive complete inundation by flood waters several times during the years of advancement of the first terrace stage to the second. It is doubtful if seedling survival for all species of poplars under inundation is the same. If the eight-day survival with complete recovery reported for *P. deltoides* by Hosner (1958) can be applied as a guideline, then forest species of southwestern Alberta riverbottoms are reasonably safe from drowning since they are seldom continuously inundated for periods longer than four days. The rapid drainage and aeration of gravel soils following flooding also prevents death by root drowning.

Water availability to the roots of trees and shrubs in mature riverbottom forest is good to excellent throughout the growing season. Spring flooding and rainfall recharge of soil moisture are coincident with early season leaf-out and photosynthesis. High water tables and water seeping through the gravels from the upstream to downstream sides of a riverbottom forest stand are evident from two observations: (1) Seepage channels originating in low spots in the gravel (i.e., "springs") were flowing or wet throughout most of the growing seasons of 1970, 1971, and 1972. During the summer of 1973, when precipitation and streamflow were below normal, these springs and seepage channels dried up by early August, but no observable woody plant damage due to drouth was noticed. In the same summer many herbaceous species in the riverbottom forest failed to develop sufficiently to flower. (2) During the course of obtaining tree trunk cores for age determinations, it was commonly noted that as the stem core was removed from the increment borer, varying amounts of tree sap would run out the end of the borer for varying lengths of time. This indicated plentiful supplies of water in these trees. Boring was done during 1971 and 1972 throughout the growing season and into autumn, even as late as mid-October after all leaves had dropped. At no time did sap fail to flow from the tree trunks. By autumn in the very dry year 1973, sap flow from trees sampled with the increment borer was very slow to nil. Corings from the driest tree trunks were still wet enough to indicate that no extreme water stress had been placed on the trees.

The river valleys originated during glacial and postglacial times, and the gravels supplied for riverbottom forest development are glacial in origin (Wyatt 1939). The higher valley terraces are seldom influenced by the river, and riverbottom forest does not develop on them. The deepening of the valley by stream erosion is a very slow process. River erosion destroys existing riverbottom communities and at the same time builds new sites

available for community colonization
(Figure 5).

Investigators of floodplain forests in
temperate North America (Lee 1945;
Ware and Penfound 1949; Shelford
1954) have been in agreement that the
pioneer stands of such forests include
poplar species. Unlike the riverbottom
forest of southwestern Alberta, other riv-
erbottom forests of more temperate cli-
mates are capable of successional develop-
ment beyond the pioneer poplar stage to
stages dominated by other species, such
as maple, ash, and elm. Maple, ash, and
elm are not part of the native flora of
southwestern Alberta, and riverbottom
forests here go through a sere of poplar
species only. These poplar-dominated
stands are capable of self-perpetuation if
the stability of the substrate permits.
Therefore the successional pathway to the
climax may be very short; the pioneer
stage to a climatic-edaphic climax with
the same species and perhaps even the
same individuals as codominants.

*Acer negundo, Fraxinus pennsylvanica,
Lonicera tartarica, Populus sargentii*, and
some exotic poplar hybrids have been in-
troduced into southwestern Alberta by
man. In spite of these introductions and
the success of the individuals, no exotic
species of woody plants have become im-
portant members of the southwestern Al-
berta riverbottom forest community. This
is true despite their importance in flood-
plain forests of other regions.

It is doubtful that any of the 291 species
of plants found in this study are truly
riverbottom forest endemics. Even the
dominant species of the four different
strata are not limited to the riverbottom
forest community. Each of the poplar spe-
cies can be found in some other habitat,
from abandoned gravel pit to home
shelterbelt. River birch and dogwood can
be found on moist sandy soil sites in
other plant communities, and snowberry,
silverberry, rose, and serviceberry are
likewise scattered across the plains and
coulees of the grasslands and aspen park-
land. Four of the nine herbaceous stratum
dominants are introduced exotics found
in a wide variety of other habitats. Of
the five native herbaceous dominants not
one is truly endemic to the southwestern
Alberta riverbottom forest community.

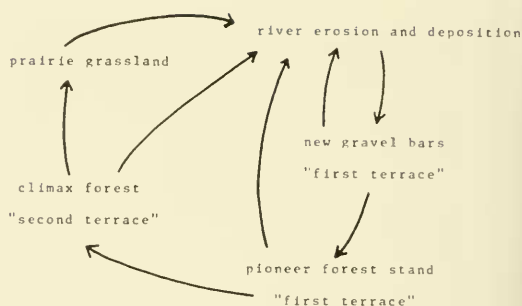The riverbottom forest poplar dom-
inants are derived partly from the adja-

Fig. 5. Successional schema for the river-
bottom forest community of southwestern Alberta,
Canada.

cent forest regions and partly from the
riverbottom forests on other streams to
the south, east, and north. Balsam poplar
(*Populus balsamifera trichocarpa*) has
followed the streams down through the
foothills from Rocky Mountain popula-
tions. Narrowleaf cottonwood (*Populus
angustifolia*) seems to have spread from
stream to stream along the edge of the
foothill zone from the south (Brayshaw
1965). Narrowleaf cottonwood has not
extended its range into the transition and
montane forests of the lower mountain
slopes, nor has it extended its range more
than casually east and north beyond Leth-
bridge.

Narrowleaf cottonwood-balsam poplar
hybrids have their population centers
within the areas of overlap of the parent
species. Brayshaw (1965) found scattered
AB hybrids in eastern Alberta well be-
yond the distribution limits of the parent
species.

Plains cottonwood (*Populus sargentii*),
a most important eastern and northern
species of floodplain forests, has been un-
able to colonize the valleys of St. Mary
River and Lee Creek. Its range does ex-
tend up Belly River to near Monarch.

Quaking aspen (*Populus tremuloides*)
is a ubiquitous species, finding any moun-
tain and foothills climate to its liking,
requiring only adequate soil moisture, and
persisting in small stands on the better
soils along river valleys where conditions
are similar to those of its population
centers in the Rocky Mountain foothills
and the northern half of Alberta.

Superficial estimates of poplar species
in pioneer stands indicated that seedlings
of narrowleaf poplar, balsam poplar, and
AB hybrids were present. Colonization of

new gravel bars does not seem to be the prerogative of any one poplar species, but this is only a tentative conclusion and must be verified through further study. In the mature riverbottom forest community a comparison of importance values for the three poplar dominants shows that there is little difference between those values for mature trees (narrowleaf cottonwood 94.5, balsam poplar 89.9, AB hybrid 110.8) and for tree reproduction (narrowleaf cottonwood 118.9, balsam poplar 90.7, AB hybrid 79.1). The differences in importance values for trees during early stages of riverbottom forest development can best be accounted for by considering that such differences are the product of the random colonization of new sites by available seeds. Succession in mature stands seems to favor one poplar slightly, the AB hybrid.

At the beginning of this study, my preconceived opinion was that narrowleaf cottonwood was unable to compete with other poplar species when forest maturity was reached. If this hypothesis were true, then it should be expected that narrowleaf cottonwood importance values would be very low in sampled mature stands of riverbottom forest. To the contrary, in each of the 10 study stands this species was a very important constituent of the mature tree stratum. Its importance value average of all stands, 94.5, made it more important than balsam poplar (I.V. 89.9) and only slightly less important than the AB hybrid (I.V. 110.8). In its ability to reproduce and perpetuate itself within the community narrowleaf cottonwood had the highest average importance value (118.9) in comparison to balsam poplar (I.V. 90.7) and the AB hybrid (I.V. 79.1).

As for absolute values, narrowleaf cottonwood ranked intermediate in density (91.5 trees per hectare) between balsam poplar (88.9 trees per hectare) and the AB hybrid (96.9 trees per hectare).

Absolute density values in tree reproduction for all stands put narrowleaf cottonwood well ahead (113.3 saplings per hectare) of balsam poplar (81.5 saplings per hectare) and the AB hybrid (65.0 saplings per hectare).

The relative success of the AB hybrid in the mature tree stratum may be due more to its greater pioneer site colonization ability and its greater average longevity than to its reproductive ability in the mature forest.

The growth in diameter of poplars on the three study streams is not nearly so rapid as the growth of other poplar species in better climates. Shelford's (1954) report of *Populus deltoides* on the Mississippi River floodplain growing to a diameter of 60 cm (24 in) in 20 years is in great contrast to the 13 and 16 cm (5 and 6 in) diameters achieved by St. Mary River, Lee Creek, and Belly River poplars in the same span of time.

Mature riverbottom forest stands that have been under a heavy grazing regime, by sheep in particular, are quite open, and one can walk through them with only minor deviations in his course (Fig. 6). Shrubs occur singly or in small patches, and between these are low-growing herbaceous species. This "English Park" appearance contrasts with other stands grazed lightly or not at all. These can be most difficult to walk through. Rose thickets, silverberry thickets, dogwood clumps, and snowberry patches can be so dense, continuous, and high as to be impenetrable to all but the most determined person.

No correlation could be found between the average age of trees in a stand and average penetrometer readings for stands. Alluvium buildup is a product of the number of over-bank floods that have occurred during the life of the terrace and these vary from stand to stand.

Observation of exposed root systems, undercut, and fallen trees shows that lateral stream migration is a major factor with which floodplain plants must contend (Lindsay et al. 1961). It is due to this erosion on the one side and deposition on the other that the floodplain owes its existence. The proportion of over-bank deposits is very small compared to channel deposits.

Island formation on St. Mary River, Lee Creek, and Belly River is rare in contrast to its importance on other streams (Lindsay et al. 1961).

In spite of the quantities of tree and shrub leaves and other herbaceous debris falling to the ground each autumn, only shallow layers of organic material have accumulated on the surface of mature riverbottom forest soils. Autumn winds

Fig. 6. Riverbottom forest stand on St. Mary River at Woodgrove Park. Clumped and thicket shrubs have been largely killed out through sustained high intensity grazing by domestic sheep.

blow the leaves away or pile them in sheltered spots. Saprophytic reduction is rapid and by leaf-out of the next spring the previous year's organic debris is little in evidence.

Mechanical damage to standing trees during over-bank flooding appeared to be minimal, based on a survey of trees in stands flooded in 1964. Trees torn away by lateral corrosion are badly abraded by transported and bottom gravels as they are tumbled downstream. Over-bank floods with slower moving water transport only the finer sands and silts that do not damage tree stems. Ice blocks were frequently pushed or floated out on to first terrace pioneer sites during unusual winter and normal early spring break up. Hydraulic pressure exerted from below by increased streamflow will break heavy ice into cakes, and these float downstream until the receding water leaves them stranded on gravel bars. The general and unsupported hypothesis is that ice does not cause appreciable damage to pioneer or mature riverbottom forest stands.

Soils under riverbottom forest stands are gravelly and topsoil layers so thin

that clearing of riverbottom forest by man for farming has never been an agricultural practice. Third and higher grassland terraces with good soil are sufficiently removed from flood danger to make farming them no more hazardous than farming the surrounding prairies.

The effect of prairie wildfire, long known to be devastating to Indian and settler alike, on riverbottom forest is unknown. Various accounts of prairie wildfires in southwestern Alberta settlement days tell of the importance of creeks and rivers in stopping the fire but do not mention what effect the fire had on trees along these streams. Poplars are not notably fire-resistant species; thus the probability of damage or death to them is great. The high percentage of bare ground under the forest probably afforded some fire protection.

Riverbottom forest stands grazed by cattle tend to remain heavily brushed. Grass forage is minimal and use is made of the forest for shade during hotter summer days. Sheep have been effective in reducing shrub densities and promoting grass cover in several riverbottom forest

stands. Heavy grazing by sheep can reduce tree reproduction to nil and promote development of a grassland which assumes dominance as the forest trees reach maturity and die.

Summary and Conclusions

Ten stands in the riverbottom forest community of St. Mary River, Lee Creek, and Belly River in southwestern Alberta. Canada, were analyzed for plant species composition during the period 1970-1973. Four vegetational strata in the community are recognized: (1) the tree canopy and its reproduction, (2) clumped shrubs, (3) thicket shrubs, and (4) herbaceous understory. Vegetational analysis methods were: (1) the point-centered quarter method for trees, tree reproduction, and clumped shrubs; (2) the line-intercept method for thicket shrubs; and (3) the quadrat method for herbaceous vegetation and unoccupied space. Data were summarized and reported in absolute terms (density, dominance) and relative terms (percent density, percent dominance, percent frequency, importance value). Similarities between the 10 stands outweighed the dissimilarities, and all 10 stands were deemed to be parts of a southwestern Alberta riverbottom forest community. Dominant species and their importance value, based on a maximum possible of 300, in the four vegetational strata of the mature riverbottom forest community were: (1) trees—*Populus* X *balsamifera* I.V. 110.8, *P. angustifolia* I.V. 94.5, *P. balsamifera* I.V. 89.9; tree reproduction —*P. angustifolia* I.V. 118.9, *P. balsamifera* I.V. 90.7, *P.* X *balsamifera* I.V. 79.1; (2) clumped shrubs—*Betula occidentalis* I.V. 171.8, *Cornus stolonifera* I.V. 72.1; (3) thicket shrubs—*Elaeagnus commutata* I.V. 80.5. *Symphoricarpos occidentalis* I.V. 59.0, *Rosa woodsii* I.V. 55.3. *Amelanchier alnifolia* I.V. 30.9; (4) herbs—*Poa pratensis* I.V. 41.9. *Medicago lupulina* I.V. 26.3. *Poa compressa* I.V. 12.1, *Chrysopsis villosa* I.V. 11.1, *Solidago mollis* I.V. 10.6. *Phleum pratense* I.V. 10.4, *Oxytropis viscida* I.V. 10.1. *Aster laevis* I.V. 9.3, *Fragaria virginiana* I.V. 7.5. All of the woody plant dominants and five of the nine herb dominants are species native to southwestern Alberta.

Succession in the southwestern Alberta riverbottom forest community follows an interwoven pattern of (1) new gravel bar, the first terrace, formed by river deposition: (2) pioneer riverbottom forest on the first terrace gravel bar floristically composed of herb species and poplar species' seedlings; (3) maturing riverbottom forest stands on first and second terraces with poplar saplings, clumped and thicket shrub invaders, and herbs; and (4) poplar-dominated climax stands capable of self-perpetuation. with mature clumped and thicket shrubs and perennial herbs. Any stage in succession may be destroyed during progressive lateral erosion by the river, and this is the usual fate of the climax forest.

Unoccupied space (bare ground and litter) accounted for 66.2 percent of the total herb stratum area.

Riverbottom forest soils range from gravel (61.1 percent rocks greater than 0.5 cm diameter and 38.9 percent sand) to sandy loams above a gravel base of unknown thickness. The sandy loam surface layer is the result of a buildup of water-borne particles deposited during infrequent over-bank flooding. Mean penetration of the soil by the penetrometer averaged 0.4 dm on gravel bar pioneer forest sites and 2.5 dm in mature forest sites. The pH values averaged 8.0 on gravel bar pioneer sites. 7.7 in mature forest soils, and 7.6 in neighboring fescue prairie grassland soils. Soil soluble salts averaged 176 parts per million on gravel bars, 458 ppm in mature forest soils, and 409 ppm in the neighboring grassland soils.

The average diameters and ages of the poplar dominants in mature riverbottom forest stands were (1) *Populus* X *balsamifera* 26.2 cm, 45 years; (2) *P. balsamifera* 21.8 cm, 38 years; and (3) *P. angustifolia* 20.8 cm. 36 years. Maximum age for any single tree of the dominant poplar species was (1) *P.* X *balsamifera* 250 years, (2) *P. angustifolia* 160 years, and (3) *P. balsamifera* 155 years. Height of the mature poplar dominants ranged from 15 to 22 meters.

The climate of southwestern Alberta is typically continental and cool. with warm summers and cold winters. Average annual precipitation is 45.8 cm (18.04 in.) with 65 percent of the total falling during the growing season.

Development of riverbottom forest is conditional on climate and substrate. The

climate determines the species that are able to survive in southwestern Alberta, and the continually forming gravel bars of the streams provide the necessary substrate. Development of the forest is correlated with May-June flooding and gravel bar formation; May-June precipitation; June-July poplar seed production, dispersal, and germination; and a high water table in the gravel substrate. The gravels are of mountain and continental glacial origin and overlie strata of Upper Cretaceous and Tertiary ages.

The riverbottom forest flora is composed of 291 species of vascular plants in 165 genera representing 50 families. Of these 291 species, 41 are woody plant species and 250 are herbs. The plant families contributing most to the riverbottom forest community flora are Compositae, Leguminosae, Gramineae, Rosaceae, Salicaceae, and Umbelliferae. These six families account for 76 (46 percent) of the genera and 172 (58 percent) of the species.

One species new to Alberta was found. Canada Plum (*Prunus nigra* Ait.) is now known from Lee Creek, 0.5 km southwest of Cardston, Alberta. Range extensions for 12 species were provided by this study. No species of plant is truly endemic to the riverbottom forest in southwestern Alberta. Plant species in the riverbottom forest community are opportunists able to take advantage of the continuing availability of new gravel bars for colonization.

The riverbottom forest community of southwestern Alberta has little economic value. Livestock grazing and shelter are the major uses with recreation as a minor use. This community provides some wildlife habitat, especially for white-tailed and mule deer.

Fire is unimportant in riverbottom forest dynamics at the present time. The greatest altering force of riverbottom forest stands is water erosion.

The riverbottom forest community of St. Mary River, Lee Creek, and Belly River in southwestern Alberta, Canada, is a unique ecological entity characterized by poplar species that have their major Alberta distribution along these streams.

Literature Cited

Barker, E. N. 1937. The Life of E. N. Barker. Lethbridge Herald. Lethbridge, Alberta, Canada.

Boivin, B. 1969. Flora of the Prairie Provinces I, II, III, IV. Canada Dept. of Agriculture, Ottawa, Ontario, Canada.

Booth, W. E. 1950. Flora of Montana. I - Conifers and monocots. Montana State Univ., Bozeman.

Booth, W. E., and J. C. Wright. 1966. Flora of Montana. II - Dicots. Montana State Univ., Bozeman.

Bouyoucos, G. J. 1936. Directions for making mechanical analyses of soils by the hydrometer method. Soil Sci. 42: 225-229.

Brayshaw, T. C. 1965. Native poplars of southern Alberta and their hybrids. The Queen's Printer, Ottawa, Ontario, Canada.

———. 1971. Unsubstantiated report of *Prunus nigra* Ait. in Alberta. Pers. comm. to the author.

Breitung, A. J. 1957. Plants of Waterton Lakes National Park. Canadian Field-Naturalist 71: 39-71.

Budd, A. C. 1957. Wild plants of the Canadian prairies. Canada Dept. of Agriculture, Ottawa, Ontario, Canada.

Canada Department of Regional Economic Expansion. 1971. Streamflow data for southwest Alberta river systems. Pers. comm. to the author.

Canada Department of Transport. 1967. Temperature and precipitation tables for prairie provinces III. Ottawa, Ontario, Canada.

———. 1969. The climate of Canada. Toronto, Ontario, Canada.

Cody, W. J., and K. Shaw. 1973. Canada Plum in southwestern Alberta. Blue Jay 31: 217-219.

Cormack, R. G. H. 1967. Wild flowers of Alberta. Queen's Printer, Edmonton, Alberta, Canada.

Cottam, G., and J. T. Curtis. 1956. Use of distance measures in phytosociological sampling. Ecology 37:451-460.

Cox, G. W. 1967. Laboratory manual of general ecology. Wm. C. Brown Co., Dubuque, Iowa.

Dyson, J. L. 1949. The geologic story of Glacier National Park. Glacier Natural History Association, West Glacier, Montana.

Ewers, J. C. 1958. The Blackfeet: Raiders on the northwestern plains. University of Oklahoma, Norman.

Flint, R. F., C. R. Longwell, and A. Knopf. 1941. Outlines of physical geology. John Wiley and Sons, New York.

Higgins, L. C. 1971. A revision of Cryptantha; subgenus Oreocarya. Brigham Young University Science Bulletin. Biological Series 13 (4).

Hosie, R. C. 1969. Native trees of Canada. Dominion Forest Service, Ottawa, Ontario, Canada.

Hosner, J. F. 1958. The effects of complete inundation upon seedlings of six bottomland tree species. Ecology 39:371-373.

Hudson, A. J. 1963. Charles Ora Card: Pioneer and colonizer. Privately printed. Cardston, Alberta, Canada.

Humphrey, H. B. 1924. The phytogeography of the Couer d'Alene flood plain of northern Idaho. Ecology 5:6-13.

Kuijt, J. 1972. Common coulee plants of southern Alberta. University of Lethbridge. Lethbridge, Alberta, Canada.

Lee, M. B. 1945. An ecological study of the flood plain forest along the White River system of Indiana. Butler University Botanical Studies 7:155-165.

Lindsay, A. A., R. O. Petty, D. K. Sterling, and W. VanAsdall. 1961. Vegetation and environment along the Wabash and Tippecanoe rivers. Ecol. Monog. 31:105-156.

Longley, R. W. 1968. Climatic maps for Alberta. University of Alberta, Edmonton.

Macleod, N. W. 1900. Picturesque Cardston and environments. Privately printed. Cardston, Northwest Territories.

Macoun, J. 1883-1909. Catalogue of Canadian plants. Geological and Natural History Survey, Ottawa, Ontario, Canada.

McClintock, W. 1910. The Old North Trail. University of Nebraska, Lincoln.

Melton, F. A. 1936. An empirical classification of flood plain streams. Geog. Rev. 26: 593-609.

Moss, E. H. 1955. The vegetation of Alberta. Bot. Rev. 21:493-567.

———. 1959. Flora of Alberta. University of Toronto. Toronto, Ontario, Canada.

Native Trees of Canada. 1949, 1956, 1961. Dominion Forest Service. Ottawa, Ontario, Canada.

Neill, C. R., and V. J. Galay. 1967. Systematic evaluation of river regime. J. Waterways and Harbors 93:25-53.

Rice, E. L. 1965. Bottomland forests of north-central Oklahoma. Ecology 46:708-713.

Rydberg, P. A. 1922. Flora of the Rocky Mountains and adjacent plains. New York Botanical Garden, New York.

———. 1932. Flora of the prairie and plains of central North America. New York Botanical Garden, New York.

Salt, W. R., and A. L. Wilk. 1958. The birds of Alberta. The Queen's Printer, Edmonton, Alberta, Canada.

Shaw, P. C. 1972. The location of "Woodgrove Park." Pers. comm. to the author.

Shaw, R. K. 1968. Guide to the woody plants of the Lee Creek Valley. Privately printed, Cardston, Alberta, Canada.

———. 1972. Guide to the woody plants of the prairies, foothills and valleys of southwest Alberta. Privately printed, Cardston, Alberta, Canada.

Shelford, V. E. 1954. Some lower Mississippi Valley flood plain biotic communities; their age and elevation. Ecology 35:126-142.

Soper, J. D. 1964. The mammals of Alberta. The Queen's Printer, Edmonton, Alberta, Canada.

Standley, P. C. 1921. Flora of Glacier National Park. Contr. U.S. Nat. Herb. 22:(5).

Ware, G. H., and W. T. Penfound. 1949. The vegetation of lower levels of the flood plain of the South Canadian River in central Oklahoma. Ecology 30:478-484.

Weaver, J. E. 1960. Flood plain vegetation of the central Missouri valley and contacts of woodland with prairie. Ecol. Monog. 30: 37-64.

Welsh, S. L. 1960. Legumes of the north-central states. Galegeae. Iowa State J. Science 35:(2).

Wistendahl, W. A. 1958. The flood plain of the Raritan River, New Jersey. Ecol. Monog. 28:129-153.

Wyatt, F. A. 1939. Soil survey of Lethbridge and Pincher Creek Sheets. University of Alberta, Edmonton.

Yang, C. T. 1971. Potential energy and stream morphology. Water Resources Research I: 311-322.